THE FUNDAMENTAL UNITS OF BIOLOGICAL TAXONOMY.

BY

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1. Introduction.

Though the species is generally accepted by present-day biologists (some geneticists excepted) as the most fundamental unit of biological taxonomy, certainly very few biologists of our days would be able to give a clear definition of what a species really is.

The main causes to that vague species-concept certainly must be sought for in historical facts. The evolution-theories of LAMARCK (1802, 1809) and DARWIN (1859) had led to a general belief in the gradual transformation of species. That »Natura non facit saltus» was doubted by very few biologists of the later half of the last century. The logical result was that species were mostly regarded merely as arbitrary divisions of the continuous and everchanging series of individuals found in nature. Of course active taxonomists did not overlook the existence of sharply and distinctly delimited species in nature — but as the existence of those distinct units disagreed with the prevailing theories, it was mentioned as little as possible, and anyhow it did not much influence the general discussion of the species-problem. Important exceptions were formed by the works of WAGNER, GULICK and ROMANES (comp. below pp. 393—394) as well as by DOLLO) 1893), BATESON (1894) and some other authors. But first the rediscovery of the Mendelian laws (1900) and DE VRIES' mutation-theory (1901) brought the principle of discontinuity to its full right again in the genetical discussion.

The vagueness of the traditional species-concept has got a very significant expression in the international rules of botanical nomenclature adopted by the international botanical congresses of Vienna 1905 and Brussels 1910. In those rules, no serious attempt at all was made to define the species-concept. The extremely vague formulation of the articles dealing with the fundamental taxonomical units is clearly shown by the following abstracts:

»Art. 10. Every individual plant belongs to a species (*species*), every species to a genus (*genus*), every genus to a family (*familia*), every family to an order (*ordo*), every order to a class (*classis*), every class to a division (*divisio*).

Art. 11. In many species we distinguish varieties (*varietas*) and forms (*forma*), in the case of parasites special forms (*forma specialis*); and in some cultivated species, modifications still more numerous; in many genera sections (*sectio*), in many families tribes (*tribus*).

Art. 12. Finally if circumstances require us to distinguish a greater number of intermediate groups, it is easy, by putting the syllable *sub* before the name of a group, to form subdivisions of that group. In this way subfamily (*subfamilia*) designates a group between a family and a tribe, subtribe (*subtribus*) a group between a tribe and a genus, etc. The arrangement of subordinate groups may thus be carried, for wild plants only, to twenty-two degrees, in the following order: Regnum vegetabile. Divisio. Subdivisio. Classis. Subclassis. Ordo. Subordo. Familia. Subfamilia. Tribus. Subtribus. Genus. Subgenus. Sectio. Subsectio. Species. Subspecies. Varietas. Subvarietas. Forma. Forma specialis. Individuum.

If this list of groups is insufficient it can be augmented by the intercalation of supplementary groups, so long as these do not introduce confusion or error.

Example: *Series* and *Subseries* are groups which can be intercalated between subsection and species.

Art. 13. The definition of each of these names of groups varies, up to a certain point, according to individual opinion and the state of the science, but their relative order, sanctioned by custom may not be altered. No classification is admissible which contains such alterations.

Examples of inadmissible alterations are, — a form divided into varieties, a species containing genera, a genus containing families or tribes.

Art. 14. The fertilization of one species by another gives rise to a hybrid (*hybrida*); that of a modification or subdivision of a species by another modification of the same species gives rise to a half-breed (*mistus, mule* of florists).» (BRIQUET 1912 p. 33.)

This vague conception of the fundamental units is still found in most taxonomical works (comp. DIELS 1921 and HITCHCOCK 1925). The differences in »individual opinion» mentioned in the rules are constantly leading to divergences between different workers regarding the right use of the various terms, the same unit being treated as a species by one author, as a subspecies by another one, as a variety by a third one, as a form by a fourth one, etc. And certainly there is little hope to attain a better stability in this respect, as long as no better definitions than those of the international rules have become generally accepted. Probably most taxonomists think that just t h e i r way of using the terms concerned should be considered the right one — but why, probably very few of them would be able to tell. The situation has grown still worse through the suggestion of various geneticists to replace the old terms of taxomomy with a lot of new ones better defined. And certainly it is no exaggeration to say, that the attaining of a stable and generally accepted system of well defined terms for the designation of the various fundamental units is one of the most urgent needs in present taxonomy.

The following attempt to a critical revision of the fundamental units of taxonomy is founded upon a synthesis of about 20 years active taxonomical field- (and museum-) work — mainly in lichens, marine algae and vascular plants — with an extensive study of taxonomical and genetical literature with a bearing upon this problem. For many years I have occupied myself with the general problems of taxonomical methodology (comp. DU RIETZ 1921 pp. 10—13, 1923 *a* pp. 235—241, 1924 *a* pp. 385—391, *b* p. 76, 1930 pp. 294—296). However, it is a great pleasure for me to acknowledge the most stimulating impulses I received during my recent sojourn in New Zealand (1926—1927) from many discussions and excursions with Dr. L. COCKAYNE and Dr. H. H. ALLAN, whose recent work on those problems could not fail to attract my intense interest. As I am going to take a good deal of the examples used in the following discussion from the flora of New Zealand, I also wish to use this opportunity to express my deep gratitude to the New Zealand Government and to all my New Zealand botanical

friends — the names of which it is impossible to enumerate here — for the neverfailing interest they took in my efforts to learn to know as much as possible of the flora and vegetation of their wonderful country. — During most of the New Zealand fieldstudies referred to below my wife, Mrs. GRETA DU RIETZ, was an invaluable collaborator.

2. The taxonomical units as concrete populations.

For many years there has been much discussion among biologists regarding the concrete or abstract nature of the various units of taxonomy. A very good summary was given in 1914 by PLATE (pp. 115—118). Many biologists have completely denied the existence of any concrete units in taxonomy except the individuals, while others have considered a l l taxonomical units as concrete. Between those two extremes there are numerous intermediate gradations. A rather common compromise accepted also by PLATE is the view that only s p e c i e s are concrete units, while all the higher units are abstract. And many modern geneticists have insisted upon the b i o t y p e s being the only concrete units existing in nature.

The following words by PLATE probably express a rather common view among those present day biologists, who have taken the trouble of thinking about those problems (comp. also KLINGSTEDT 1928).

»Die Worte Art, Gattung, Familie usf. haben einen doppelten Sinn; sie bezeichnen einmal B e g r i f f e v o n G r u p p e n und sind als solche wie alle Begriffe abstrakt; sie bezeichnen aber auch die realen Objekte, welche diesen Begriffen zugrunde liegen, also I n d i v i d u e n k o m p l e x e, und solche Komplexe sind natürlich ebenso real, wie die Individuen, aus denen sie sich zusammensetzen. Diese Individuenkomplexe sind voneinander insofern verschieden, als derjenige Individuenkomplex einer Art völlig unabhängig ist von der menschlichen Analyse und daher objektiv in der Natur existiert, während die übergeordneten Individuengruppen (Gattung, Familie usf.) nicht durch sich selbst, sondern nur durch den vergleichenden und überlegenden Verstand des Menschen gebildet werden. In diesem Sinne ist die Art etwas Reales, während die Gattung, die Familie, überhaupt die höheren Gruppen abstrakter Natur sind.» (PLATE 1914 p. 118.)

In modern genetical literature species and their subordinate units are often spoken of as p o p u l a t i o n s (= PLATE's »Individu-engruppen») — certainly a very sound and stimulating method of treatment. In a previous paper (Du RIETZ 1930 pp. 293—296) I have proposed to apply the population-concept to all sorts of taxonomical and plantsociological units, a course that I am going to take also in the following discussion. Thus I am going to treat a l l the various units of taxonomy discussed below simply as concrete populations, leaving the discussion of the possibly abstract nature of the c o n c e p t s aside to those biologists more interested in formal logic than myself. Far more important than those purely theoretical discussions is, according to my opinion, the problem of the definite or arbitrary nature of the border-lines between the populations accepted as units (Du RIETZ 1923 a). But of course even a most arbitrary delimitation cannot take away the concrete nature of the population we are dealing with (comp. HALL and CLEMENTS 1923 p. 9). Nor may we forget the g e n e a l o g i c a l c o n t i n u i t y of a species as is often done by authors advocating a purely abstract species-concept (comp. KLINGSTEDT 1928).

3. The individual.

The most elementary unit of taxonomy is the individual. The limits of an individual are not always easy to define, but I think most biologists of the present day agree that the soundest definition is the physiological one, *i. e.* that the main criterion of an individual should be its physiological autonomy. Thus in cases of vegetative propagation a new individual is formed with the break of the connection with the mother-plant. Theoretical and practical complications arise in several cases, especially in the case of vegetative segregation and in colonies of closely connected individuals. I think, however, that we may leave those cases aside in the following discussion. After the introduction of the clone-concept (comp. below) certainly nobody will share the opinion of GALLE-SIO (1816) and HUXLEY (1855), that every clone should be considered o n e individual, a view rather widespread among earlier authors. As to the various individual-concepts of classical morphology compare HAECKEL 1866 pp. 241—374.

4. The clone.

A clone (WEBBER 1903, SHULL 1912 a and b, JOHANNSEN 1913) is a population consisting of the vegetative (asexual) descendants of one individual.

There has been some doubt whether a clone must consist only of genotypically identical individuals or if also individuals formed by vegetative segregation (»bud-mutation» etc.) may be included in it. SHULL (1912 a pp. 28—29) primarily adopted the first view, but later on (1912 b p. 183) went over to the second one, making his clone-concept a »purely genealogical» one. JOHANNSEN (1913 pp. 200 and 209) joined the latter view, which appears to be the prevailing one among modern geneticists (comp. WINGE 1928 p. 50). Practically, the matter is of minor importance, but obviously this clone-concept is useless as a taxonomical unit. In order to avoid confusion and uncertainty, it may be recommended to use the term »pure clone», when dealing with clones as taxonomical units, $i. e.$ when genotypical homogeneity is postulated.

A special type of clones of great importance for taxonomy is the apomictic one, formed by apomictic propagation of one individual.

The investigations of modern geneticists have clearly proved that the various individuals of a clone are genotypically identical (vegetative »mutations» excepted). Thus a clone apparently is a taxonomical unit of extreme homogeneity. At least many of the species of *Taraxacum* and of *Hieracium* subgenus *Archieracium* described by Scandinavian taxonomists probably are pure clones (comp. below pp. 358 and 362).

5. The pure line.

A pure line (JOHANNSEN 1903) is a population consisting of the individuals formed by strictly autogamous reproduction of one homozygotic individual.

There has been some doubt wether only populations formed by autogamous reproduction of one homozygotic individual should be called pure lines, or if that concept may be extended also to populations including heterozygotic individuals (LEHMANN 1914 pp. 286—287). However, it appears quite clear that the term »pure

line» must be maintained in the sense of JOHANNSEN — if not, we would have to invent a new term for the concept of JOHANNSEN, as we certainly cannot do without it. On the other hand, it appears that we have little need of LEHMANN's extended »pure line»-concept. Practically, the matter is of little importance, as strictly autogamous reproduction within few generations leads to (at least practical) homozygosity (JENNINGS 1912 p. 487 etc., Jo-HANNSEN 1913 pp. 484—485, 496—499, comp. also for instance NILSSON-EHLE 1915 p. 35, LOTSY 1916 pp. 68—75, BAUR 1919 pp. 311—312, HAGEDOORN 1921 pp. 115—118).

As JOHANNSEN (1903, 1913 etc.) and others have shown, a pure line is a unit of the same homogeneity as a clone, i. e. all individuals of one pure line are genotypically identical, provided that no »mutation» takes place within it. However, the pure line-concept of JOHANNSEN is a purely genealogical concept, i. e. if a mutation takes place, the descendants of the genotypically deviating individual arisen through this mutation are included in the same pure line, which thus loses its genotypical homogeneity (comp. JOHANNSEN 1913 pp. 209—210, SHULL 1912 a pp. 28—29). As a t a x o n o m i c a l unit, the pure line thus is as useless as the clone. For taxonomical use, a concept corresponding to that of the »pure clone» would be necessary, i. e. a concept including only pure lines of genotypical homogeneity. In the following discussion I am going to designate this concept by the term »pure line *sensu stricto*» (or »pure line *s. str.*»).

Good examples of pure lines of apparent taxonomical value are furnished by the »petites espèces» of *Erophila* described by A. JORDAN (1864, 1873) and ROSEN (1889, 1910, 1911, 1925, comp. WINGE 1926 a[1]). However, as a b s o l u t e autogamy appears to be at least extremely rare in nature (comp. LOTSY 1916 pp. 77—78), the taxonomic value of pure lines appears to be rather restricted. At least in most pure lines a cross with another one sooner or later will happen, giving rise to a lot of new pure lines and thus increasing their number so much that their recognition as taxonomical units will be a rather hopeless task — especially if many of those pure lines are phenotypically overlapping and practically indistinguishable from each other (SHULL 1929 b).

[1] According to LOTSY (1926), some of those may be apomictic clones, in spite of WINGE's criticism of BANNIER's (1923) attempt to prove the existence of apomixis in *Erophila*.

6. The biotype.

A b i o t y p e (Johannsen 1909) i s a p o p u l a t i o n c o n s i s t-
ing of individuals with identical genotypical
c o n s t i t u t i o n.[1]

The term biotype, now in general use, was not immediately
generally accepted by geneticists, some of them preferring for a
long time to use Johannsen's term »genotype» also in this sense
(comp. for instance Lotsy 1916, Schmidt 1917, Heribert-Nilsson
1918). In some previous works (Du Rietz 1921, 1923 a) I followed
those authors, while my present treatment of all taxonomical units
as concrete populations of course makes the accepting of Johannsen's
distinction between »genotype» and »biotype» quite necessary.
(Comp. also Jennings 1911 and Shull 1912 a.)

As every pure clone and every pure line s. str. consists of one
biotype, the biotype in exclusively vegetatively propagating or
strictly autogamous populations is a unit of apparent importance
for taxonomy. In strictly allogamous populations without vegeta-
tive reproduction, however, there is little chance that any biotype
is represented by more than one individual (at least at the same
time), on account of the very great number of possible combi-
nations of genes. This has been pointed out by many authors
(comp. for instance Lehmann 1914 p. 291, Lotsy 1925 a p. 29); a
good example is furnished by the human population. In those
cases the biotypes are apparently of little taxonomical importance,
as biotype and individual will become practically synomymous.
Intermediate cases are found in populations with both vegetative
and allogamous or with both autogamous and allogamous pro-
pagation.

A biotype may be either h o m o z y g o u s or h e t e r o z y g o u s.

According to our present knowledge, there is probably not much
chance to find completely homozygous biotypes in other popula-
tions than strictly autogamous ones (Johannsen 1913 p. 627). This
means that the only really homozygous biotypes existing will be
those forming pure lines — and even the homozygosity of those
is now seriously doubted by Lotsy, probably with full right
(Lotsy 1925 a p. 27). In a series of papers published in the

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[1] In his earlier works (1905) Johannsen used the Danish equivalent of »bio-
type» (»livstype») as a synomym for both his later terms »genotype» and »bio-
type». The form »biotype» was first used in 1906 (comp. Shull 1912 a p. 27).

years 1912—1916, however, LOTSY claimed that the homozygous biotypes were the real fundamental units of taxonomy, and therefore the only units worthy of being called s p e c i e s. Theoretically, it was not LOTSY's intention to make his new species-concept synonymous with JOHANNSEN's p u r e l i n e (*s. str.*), as he at that time apparently expected absolute homozygotes to occur also in allogamous populations[1]. He vigorously defended himself against the accusal of LEHMANN (1913, 1914 *a*, *b*) of having proposed a restriction of the term »species» only to the pure lines (LOTSY 1914 *b* pp. 614—616) and clearly declared, that »keineswegs alle Arten reine Linien sind». Nevertheless, it has become a habit among geneticists to polemize against the absurd proposition of LOTSY to call only pure lines species — without mentioning anything about LOTSY's first supposition that species in his sense were common also in allogamous populations (HERIBERT-NILSSON 1918 pp. 136—137, HAGEDOORN 1921 p. 190, TURESSON 1929 *a* pp. 325 and 332). Certainly this is not quite fair, as a good deal of the absurdity in LOTSY's t h e o r e t i c a l species-concept is constructed by those authors themselves. Practically, they probably are quite right in their belief that species in LOTSY's sense will be formed only in pure lines. But in order to give a clear view of LOTSY's species-concept it is absolutely necessary to point out that its founder expected it to be generally applicable both in autogamous and allogamous populations. And even if this supposition may look absurd in the light of our present knowledge, we must not forget that it may have been a different matter in 1912—1916.

In his polemics against LOTSY, LEHMANN (1914 *b*), who wanted to retain the term species in its old sense, proposed the term »isogene Einheit» as a designation for LOTSY's »species». But the ambiguity of that term appears to have been felt by LEHMANN himself, for in one place (1914 *b* p. 291) he replaces it with »das Isogenhomozygotische». Nevertheless LEHMANN's term »isogene Einheit» has been accepted by LOTSY (1920 p. 181) as a substitute to his »species», the latter term being completely avoided in LOTSY's more recent papers. Another synonym for the same concept is RAUNKIAER's »genospecies» (RAUNKIAER 1913, 1918). For our present need, no other term for that concept than »homozygous biotype» appears to be necessary.

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[1] Later on, LOTSY gave up this belief and went over to the extreme contrary, namely to the doubting of the existence of a n y absolutely homozygotic biotypes in nature (1925 *a* p. 27) even in pure lines.

As a complement to his new species-concept, LOTSY proposed to call all h e t e r o z y g o u s biotypes »hybrids» — which meant the introduction of a quite new sense also for this venerable term. Also this proposition must be seen in the light of LOTSY's belief in the common occurrence of homozygous biotypes (species *sensu* LOTSY) also in allogamous populations. Certainly it was not LOTSY's intention to propose to call e v e r y biotype in an allogamous population a hybrid — as has turned out to be the practical consequence of his hybrid definition. Also RAUNKIAER (1918) applied the same hybrid- (or »bastard»-) concept.

It is of great importance for the right understanding of much of the recent literature on species and hybrids to keep in mind the real origin of LOTSY's new application of the terms »species» and »hybrid». That LOTSY's species-concept was radically different from the traditional one, has been realized by all authors. That just the same thing must be said of his hybrid-concept, has apparently been overlooked by many.

Theoretically, two or more biotypes may be morphologically absolutely alike but still have different genotypical constitutions, possible to reveal only by genetical analysis. Such biotypes would form an i s o r e a g e n t in the sense of RAUNKIAER (1918). According to RAUNKIAER, the isoreagent is »die letzte Einheit der Systematik». The practical need of this concept, however, appears rather doubtful. In strictly allogamous populations, as mentioned above, there is little chance for any biotype to be represented by more than one individual (or one clone). Probably the chance that two individuals belong to biotypes with absolutely identical morphological appearance is not much greater. Anyhow, what we know about the human population does not give much hope to find two such individuals.

7. The form.

A f o r m (*forma*) is a p o p u l a t i o n o f o n e o r s e v e r a l b i o t y p e s o c c u r i n g s p o r a d i c a l l y i n a s p e c i e s - p o - p u l a t i o n (n o t f o r m i n g d i s t i n c t r e g i o n a l o r l o c a l f a c i e s o f i t) a n d d i f f e r i n g f r o m t h e o t h e r b i o - t y p e s o f t h i s s p e c i e s - p o p u l a t i o n i n o n e o r s e v e r - a l d i s t i n c t c h a r a c t e r s.

The term »form» has been used by taxonomists in so many different senses, that the possibility of uniting taxonomists in the use of that term proposed above appears rather doubtful. If this proposition should fail to become generally accepted, the best thing to do will certainly be to abandon the term »form» altogether (except perhaps in a very general sense, as proposed by COCKAYNE 1928 p. 7, 1929 p. 23). But it would not be easy to find a better term for the concept concerned — nor to get this new term universally accepted. The term »aberration», now frequently used by zoologists about in the same sense (SEMENOV-TIAN-SHANSKY 1910, DOBRZANSKY 1924, RENSCH 1929), is used by WINGE (1928 p. 243) and other modern geneticists (e. g. CLAUSEN 1927 p. 253) for a quite different concept (chromosome-mutation). Another newly established synonyme is »exotypus» (REMANE 1928, comp. RENSCH 1929 p. 10). Very often also the term »variety» has been used in this sense.

In many taxonomical works (comp. for instance ENGLER 1916 p. 4) we find the term »form» used for the designation of what is now generally called »modification» (NÄGELI 1865 pp. 277—278, 1884 p. 264, LOTSY 1916 p. 28, BAUR 1919 p. 9, DIELS 1921 p. 175) or »epharmone» by COCKAYNE and ALLAN (1927 p. 263, comp. also COCKAYNE 1928 p. 7, 1929 p. 22), i. e. units of purely p h e n o t y p i c a l nature. For this concept, however, the term m o d i f i c a t i o n appears to be so well established in the literature of the present day, that we certainly do best in sticking to it. That I am not giving the modification a place among the »fundamental units of taxonomy», is due to my strong conviction of the absolute futility of describing and naming modifications in taxonomical works. If we describe and name one modification, we could equally well describe and name thousands or millions of them. Of course exact studies of the phenotypical variability of biotypes may have their given place in botanical science — but such studies should certainly be made in a way quite different from that of describing and naming modifications as taxonomical units.

According to the definition of the form given above, it would be theoretically possible to describe every morphologically distinguishable biotype of a species as a form. If we keep in mind the little chance of any biotype being represented by more than one individual (or clone) in allogamous populations, the futility of this task is easily seen. The describing and naming of single

biotypes within a species can certainly only be taken into consideration when one biotype is represented by a great number of individuals, as is the case in clones and pure lines.

In allogamous populations with vegetative propagation leading only to the formation of s m a l l clones it is obviously equally futile to describe and name each of those clones as it would be to describe each individual in an allogamous population without vegetative propagation. The formation of such small clones is a very common process in nature. An easily observed example is that furnished by the *Anemone nemorosa*-population around Upsala, in which a careful observation everywhere reveals clones one or a few square meter large, and distinctly differing from each other in colour (some are anthocyaninic and some are not), the form and size of the sepals, etc.

If sexual reproduction remains unchecked, there will be little hope for such clones to develop to larger monobiotypic populations worthy of special descriptions and names. But if the clone-forming biotype has lost its power of sexual reproduction completely or partly, the clone will easily develop into a monobiotypic population of sufficient size to be recognized by taxonomists. If the power of sexual reproduction is only partially lost, as in the cases of facultative apomixis described in *Hieracium* subgenus *Pilosella* (OSTENFELD 1910, 1912, 1919, ROSENBERG 1917, comp. also TÄCK-HOLM 1922 pp. 313, 352—353), the apomictic clones may become large enough to be distinguishable as distinct f o r m s, but between those clones crossing takes place often enough to make it impossible to treat them as separate species. Quite different is the case if the power of sexual reproduction is completely lost. In this case many clones may develop into sharply delimited monobiotypic populations large, constant, and permanent enough to be easily recognized by taxonomists as distinct s p e c i e s, each with its characteristic distribution-area. The best known examples of such populations are furnished by apomictic species in the section *Vulgata* of *Hieracium* subgenus *Archieracium* (comp. below pp. 358 and 362).

However, it also happens that a clone completely lacking the power of sexual reproduction lacks the vitality needed for growing out into a population large, constant, and permanent enough to be treated as a new species. Good examples of such clones are furnished by lichens. Of many lichen-species normally pro-

ducing apothecia but no soredia there are found soredia-producing forms without apothecia, occuring sporadically as very small isolated clones in the great population formed by the species concerned, and obviously of slight vitality and ephemeral appearance, as larger clones are never found. In a previous paper (Du Rietz 1924 *a* pp. 386—388) I have described several such clones (or groups of near related clones) as v a r i e t i e s, while similar clones (or groups of clones) of somewhat larger size and apparently of somewhat greater vitality were described as s u b s p e c i e s (l. c. pp. 388—389). With the terminology proposed in this paper, both types of clones must be called f o r m s only. As will be shown further below, there are also found soredious clones with great vitality and large continuous distribution-areas, having the typical appearance of s p e c i e s and being separated by taxonomists as such.

Analogous to the clones with retained power of sexual reproduction are probably most of the pure lines occuring in wild plant-populations. As absolutely pure autogamy is hardly found in nature, there is little chance for any pure line to grow out into a real species, but very often it may grow out unspoilt by crossing into a population large and distinct enough to be distinguished as a good f o r m. Good examples of such pure lines easily distinguishable in nature are the »petite espèces» of *Erophila* mentioned above (p. 339). Several of those pure lines are often found together; crossing is apparently rare in nature but easily performed artificially, resulting in a large number of new biotypes (Rosen l. c.).

Such distinct m o n o b i o t y p i c f o r m s as mentioned above from autogamous or asexual populations are lacking completely in typically allogamous populations. If we want to divide such populations into forms, we will have to deal with p o l y b i o · t y p i c f o r m s, *i. e.* with groups of biotypes kept together by certain characters lacking in other groups. Such polybiotypic forms have no genealogic continuity; they simply consist of a lot of s i m i l a r biotypes arising independently of each other in the everchanging stream of intercrossing biotypes, and disappearing again when crossed with biotypes belonging to other forms of the same populations (if not disappearing because of lacking vitality or sterility, as is often the case in the most aberrant forms of a species-population). Thus the polybiotypic form can scarcely be said to be a n a t u r a l unit, being far more an a r t i f i c i a l

means of studying the polymorphy of a given species-population. We should not forget that when choosing a system for naming and describing polybiotypic forms.

In many cases we only want to keep apart the most aberrant forms of a species-population, leaving the rest of the population undifferentiated under the name of »the main form», »f. *typica*», or similar designations. Thus we often want to note the occurrence of sporadic white-flowering forms in a species with normally coloured flowers, or of forms with laciniate leaves in species with normally entire leaves. Such forms are now often described and named in the same manner as species and other units of higher rank, *i. e.* they are given an arbitrarily chosen Latin name and a short Latin diagnosis. Certainly this is a very unpractical method. Much better is the (also common) method of naming all white-flowering forms of normally coloured-flowering species »*forma floribus albidis*» (»*f. flor. alb.*»), *i. e.* of choosing a stereotyped formula for all the analogous forms of different species. That this method is practically applicable, is due to the remarkable parallelism in polymorphy found in the most different species of the same class of the vegetable system, and often quoted in modern literature as »VAVILOV's law of homologous variation» (VAVILOV 1922, comp. also BAUR 1919 pp. 293—294, DU RIETZ 1921 p. 13, PHILIPTSCHENKO 1926 pp. 63—81, SEYBOLD 1927, TROLL 1928 pp. 90—91, HALL 1928 p. 8). Also for the naming of t e r a t o l o g i c a l forms this method appears very suitable.

This method, which really implies a naming of the characters of the forms rather than of the forms themselves, certainly is much in advance of the ordinary practice of taxonomists, *i. e.* that of naming each form by an arbitrarily chosen name, difficult to invent and difficult to remember, and describing it with a diagnosis (a good system of character-naming, of course, makes any description superfluous). It is equally applicable when we want more than distinguishing the most aberrant forms, *i. e.* when we want to divide the whole species-population into forms suitable for helping us to study the polymorphy of that population. In the taxonomy of *Sphagnum,* this method was proposed already by RUSSOW (1888), and is now commonly used by sphagnologists. Certainly it has done much for simplifying the taxonomy of this polymorphic genus. However, a good part of the *Sphagnum*-forms designated in this way may be mere modifications.

In most cases, however, it will prove necessary for the intensive study of the polymorphy of species-populations to invent a special system for the division of the species-population concerned into suitable forms and for the naming of those forms. Good examples for such practical systems are furnished by H. E. PETERSEN's studies of the polymorphy in the species *Anthriscus silvestris* (1914, 1922) and *Pimpinella saxifraga* (1921), and also by CRAMPTON's monographs of the land-snail genus *Partula* in the Society and Mariana Islands (1917, 1925 a, b). In *Anthriscus silvestris*, PETERSEN distinguished 16 »main groups of forms» marked by Latin names (*Brevisecunda, Latior Brevidivisa, Latadivisa* etc.), the distribution of which was studied statistically; in each group he distinguished and named a number of »forms» (*Brevisecunda media, Brevisecunda Longibrevis media,* etc.). In a similar way, CRAMPTON divided his species of *Partula* into a number of »color-classes»[1] (sometimes those were grouped to »color-orders»), which were used as units for the statistical studies of the regional variability of the polymorphy of the species. In many cases it may prove practical not to give the forms any names at all, but simply divide the population into variation-classes marked by numbers (SIRKS and BIJHOWER 1919, PETERSEN 1924, 1926), or by letters symbolizing the main characters, as was done already by COUTAGNE 1895 in his studies of polymorphic mollusca (comp. BATESON 1913 p. 126) as well as by RAUNKIAER (1925) in his study of the polymorphy of a Danish *Crataegus*-population. It may also often be practical to study the polymorphy of the different organs separately, using a »dynamic system» in the sense of HAYATA (1921 a, b, 1928 b, c, comp. below p. 409). The species *Picea excelsa*, for instance, is often divided into one series of forms according to the form of the cone-scales and other series of forms according to the ramification, the needles etc. (comp. SYLVÉN 1916 a pp. 112—152).

In practical taxonomy, such intense analyses of the polymorphy within a species-population as mentioned above is mostly out of question, the average taxonomist having to be content with distinguishing the most conspicuous forms within each species. As a matter of fact, even those most conspicuous forms of a species are often completely neglected by taxonomists, as long as they are regularly occurring together, thus being normal characteristics

[1] Analogous to the »color-patterns» or »elementary patterns» distinguished by PILSBRY and COOKE (1912—1914) in Hawaiian *Achatinellidae*.

of every part of the species-population concerned. Very few taxonomists, for instance, take the trouble of distinguishing and naming the two colour-forms of *Orchis sambucina* (in the floristic handbooks those are only rarely mentioned as f. *typica* and f. *purpurea*) — it is simply considered characteristic for the species that both those forms are regularly found together. More or less analogous cases are offered by anthocyaninic and non-anthocyaninic forms of many other species: sometimes they are named by taxonomists, sometimes not. Analogous forms differing in the shape of the leaves, in the villosity etc. are, as a rule, estimated somewhat higher, and are mostly mentioned in the floristic handbooks as f. *latifolia* and f. *angustifolia*, f. *glabra* and f. *villosa*, etc. But only if the forms concerned show marked differences in their distribution, *i. e.* tend to the formation of more or less pure populations, they attract the interest of taxonomists in a more profound way. In this case, however, they approach the next stage in the series of taxonomical units, namely the variety.

As the near relation between two morphologically distinct forms of one species-population may be very difficult to recognize except by a close field-study of the living population, various forms of the same species (and even of the same variety) have often been described as separate species in traditional museum-taxonomy. Good examples are furnished by many of GULICK's species of Hawaiian *Achatinellidae*, shown by PILSBRY and COOKE to be mere forms of the same species. And if the two colour-forms of *Orchis sambucina* had been growing in an exotic country without local botanists and sent to a European museum in dry herbarium-specimens (or even in living specimens to a botanical garden), they would probably have been described as two good species. The danger of mistaking forms for taxonomic units of higher rank may be avoided only by f i e l d s t u d i e s of the population concerned, or to some extent by very large and properly labelled collections demonstrating the polymorphy in each locality.

8. The variety.

A v a r i e t y (*varietas*) i s a p o p u l a t i o n o f o n e o r s e v e r-a l b i o t y p e s, f o r m i n g a m o r e o r l e s s d i s t i n c t l o-c a l f a c i e s o f a s p e c i e s.

With the variety we have reached the lowest unit in the series of taxonomical units forming more or less closed intercrossing populations or s y n g a m e o n s (LOTSY 1918, 1919 *a, b,* 1921, DANSER 1924). While the various forms of an (allogamous) variety constantly cross with each other, thus presenting a more or less ephemeral appearance, the variety itself is subject to crossing with other varieties only in the transition-zones to them.

The occurrence of more or less distinct local facies of a species-population (»local races») is a fact wellknown to biologists since long ago. Many of the »petites espèces» of A. JORDAN and his followers were such local races, while others probably were mere forms in the sense defined above. However, it was first by the intense study of the polymorphy of animal species-populations started towards the end of the last century, that the differentiation of species into local races became more intimately known. Thus GULICK (1872—1905), COUTAGNE (1895), and MAYER (1902) demonstrated the marvellous local differentiation in Mollusca, while HEINCKE (1898) described »Familien oder Stämme»· of the herring, regarded by him as forming »die erste Gruppe des natürlichen Systems und der notwendige Ausgangspunkt aller Untersuchungen über 'die Entstehung der Arten'». In 1910, SEMENOV-TIAN-SHANSKY proposed the term »natio» for such »besonders kleine lokal-geographische Einheiten» within a species. Somewhat later LLOYD (1912) described a most remarkable local differentiation of Indian rats, the rat-population of each house forming a more or less distinct local facies of the species — a result later confirmed by HAGEDOORN (1921) for other countries. In a series of important papers, SUMNER (1915, 1917, 1918, 1920, 1923, 1924) demonstrated the differentiation of the California deer-mouse (*Peromyscus maniculatus*) not only in the main geographical races called subspecies but also in a large number of genotypically fixed local races. J. SCHMIDT (1917) probably was the first author to apply the concepts and terms of modern genetics upon such local races, showing that each local race of the fish-species *Zoarces viviparus* consisted of a great number of intercrossing biotypes, »the average characters of the races in first line being only the statistical expression for a different mixture of various genotypes[1]» (p. 334). SCHMIDT also pointed out (p. 333), that if his interpretation of his *Zoarces*-ana-

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[1] = biotypes (comp. above p. 340).

lyses was right, »there can hardly be any doubt that what has been found for *Zoarces* has a g e n e r a l validity for a l l populations of a l l fish-species etc.» Analogous results were obtained by CRAMPTON (1917, 1925 *a, b*) in his studies of Pacific *Partula*-species, each »colony» (= variety in our sense) consisting of a great number of »color-classes» in proportions differing from those of all other colonies. — A similar differentiation of a p l a n t-species into local populations widely differing from each other in the percentage of the various »groups of forms» composing the species was shown in 1914 by H. E. PETERSEN (comp. also PETERSEN 1922) for *Anthriscus silvestris*. Some years later, analogous results were obtained by TURESSON (1922) in his study of the local races of *Hieracium umbellatum* differentiated in various parts of the coast of Skåne in South Sweden.

The works mentioned above are only some of the main ones in this field of study. The differentiation of species into local facies, each containing a great number of intercrossing biotypes, has now been demonstrated by so many authors (especially zoologists, comp. besides those mentioned above especially GOLDSCHMIDT, SEILER and POPPELBAUM 1920), that there is little reason to doubt that a closer investigation will reveal a similar local differentiation in most sexual species of both plants and animals.

As to the terminology of those local races, the term »natio» (SEMENOV-TIAN-SHANSKY 1910) has been used by several zoologists, especially in Russia. It has the great advantage of never having been used in any other sense, but appears to be too little known to have much hope to become generally accepted. The term »jordanon», proposed by LOTSY in 1916, according to LOTSY's original definition (1916 p. 27) would be about synonymous with RAUNKIAERS »isoreagent» (comp. above p. 342), but, on the other hand, it was explicitly proposed by LOTSY »to replace the term species in the Jordanian sense, viz.: mikrospecies, elementary species etc.» It is not quite clear from LOTSY's own works in what sense the term »jordanon» is p r a c t i c a l l y used by its originator, but probably it may be considered as about synonymous with our »form». By COCKAYNE and ALLAN (1927, comp. also COCKAYNE 1928, 1929) the term »jordanon» is used both synonymous to our »form» and to our »variety». PHILIPTSCHENKO (1927), on the other hand, proposes to use »jordanon» for all units intermediate between the biotype and the »Linneon» (= the species), and

suggests to distinguish between »Jordanon I Ordnung» (= our subspecies) and »Jordanon II Ordnung» (= our variety). Thus the term »jordanon», in spite of its youth, has already been used in quite as many different senses as the old term »variety» has, and cannot be given any preference from that point of view.

As mentioned above, the term »variety» has been used very often simply as a synonym to our »form». It has also been used to designate a superior unit of the same character, *i. e.* a more collective form or a group of similar forms. However, we also find it used in taxonomical literature as a designation of a geographically limited part˙ of a species-population. In the system of taxonomical units proposed in 1916 by the grand old man of present-day taxonomy, ADOLF ENGLER, we find the term »form» used to designate mere modifications, and »Subvarietät» about as a synonym to our »form», while three units of a more regional character (geographically limited facies of the species-population) are recognized: 1. »Subspecies». 2. »Varietät» und 3. »Rassenvarietät oder Proles (*var. proles*)». None of the three terms last mentioned is used for units of purely local character, all of them far more corresponding to our »subspecies» — or partly even to our species, as the species-concept of ENGLER is an extremely wide one.

The term »variety» has thus been used in taxonomy for units of the most different rank, ranging from our forms to our subspecies. I fully realize the boldness of my proposition to restrict that term to a unit of more intermediate rank, namely to the more or less l o c a l facies of a species-population. However, if we want to keep the old term »variety» for any of the units of modern taxonomy, this will probably be the only one possible. If my proposition should fail to become generally accepted, the best way will possibly be to abandon the term »variety» altogether, taking our refuge to SEMENOV-TIAN-SHANSKY's term »natio» for the unit in question.

As has been pointed out clearly by HAGEDOORN (1921 pp. 136—139), distinct varieties in our sense are formed only in species consisting of comparatively stationary individuals. In species consisting of more or less rapidly migrating individuals no distinct varieties are found. The differentiation of varieties must thus be due to a certain amount of i n b r e e d i n g, causing a »reduction of the Total Potential Variability»[1] in the sense of HAGEDOORN.

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[1] = »the number of genes in respect to which an individual or any group

The inadequacy of the common belief in selection as the main acting force to the differentiation of varieties has been shown in a most suggestive way by HAGEDOORN. To HAGEDOORN we also owe the explanation of the a u t o m a t i c reduction of potential variability or polymorphy that takes place quite independently of any sort of selection in any allogamous population more or less effectively cut off from crossing with populations of a different genotypical constitution. This explanation may be summarized in the following way:

1. In a group of freely crossing organisms, »we can very easily show mathematically that, supposing every mating to result in an equally large number of offspring, and assuming an uninterrupted steady increase in numbers, the potential variability remains undiminished. JENNINGS and PEARL have worked out these calculations very thoroughly. However, how does it work out in reality? Is it possible that there is an automatic reduction of variability in freely crossing populations, of the same nature as the very great reduction in self-fertilized organisms and in inbred series, slower, but still appreciable?

In the first place it is obvious, that the multiplication of any group of organisms cannot proceed indefinitely. A few heterozygotes in a mixture of organisms, of which the majority are homozygous will continue to exist as long as multiplication is unchecked. But, wherever the group is continued from a fraction of the number of individuals, or where a colony is started by a few individuals, the chance of the heterozygotes to be included in the group, or to have heterozygous children included, is proportionate to their frequency. Heterozygotes will produce homozygotes, but not the reverse.

The group of organisms chosen by fate to become the parents of the next generation is usually, but always occasionally, considerably smaller than the number of individuals of their species. Every case in which rare individuals, having genes, not present in the majority, or in which rare individuals being impure for,

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of individuals is not pure, homozygous» (HAGEDOORN 1921 p. 104). For the same concept DANSER (1929 *a, b*) uses the term »potential polymorphy». As the term »polymorphy» is tending to replace »variability» in the literature of the present day as a designation of the »gruppenweise Variabilität» (PHILIPTSCHENKO 1927) of a population (comp. COCKAYNE and ALLAN 1927 p. 239), I am following DANSER in this respect.

or lacking in genes, common property of the majority, happen to be excluded from the number of pro-creating individuals, the total potential variability is lowered.

This, in our opinion, is the most important gain in knowledge which we owe to MENDEL's work, and to the biomechanical interpretation of his work. Reduction of potential variability, in other words purity of species is automatic, and not dependant upon any sort of selection.» (HAGEDOORN 1921 pp. 119—120.)

2. If the population concerned is divided into two parts, and those parts are isolated from each other in absolutely identical habitats, there are very great chances that the reduction of potential polymorphy taking place in those isolated parts of the population leads to different results, as 1) the initial genotypical composition of the two parts is hardly ever absolutely identical, some genes probably being stronger represented in one part than in the other, thus having greater chances to survive and to become homozygous in the first part than in the other, and 2) even if a certain gene is equally represented in both parts, its fate in those parts is largely determined by pure chance, in extreme cases leading to its elimination in one part and its homozygosity in the other. Of course this automatic differentiation may be increased by selection, if the habitats of the two parts differ from each other.

3. Even if no complete isolation occurs within a population, the reduction of potential polymorphy easily leads to different results in different parts of the population, causing a differentiation of the population into subordinate units, if intercrossing between more distant parts of the population is prevented by the stationary habit of the population. But while in cases of complete isolation the differentiation results in units more or less sharply delimited from each other (= species), it results in the latter case only in the formation of more or less intergrading units (= subspecies and varieties).

At last it must not be forgotten that in plant-populations the reduction of potential polymorphy, and thus also the differentiation of varieties, is very often hastened by a certain amount of autogamy, or by the formation of clones.

As to the practical study of varieties, most taxonomists certainly agree that Latin names and diagnoses are of little use for those units. A variety is best named by its locality, and is best described by a statistical survey of the forms constituting it (comp.

above p. 347). Very good examples for the various modern methods
of studying varieties are furnished by PETERSEN's monographs of
Anthriscus silvestris and other Danish plant-species (1914—1926,
comp. above p. 347), by CRAMPTON's monographs of Pacific *Partula*-
species (1917, 1925 *a*, *b*) and by E. ANDERSON's (1928) investigation
of two North American species of *Iris*.

9. The subspecies.

A subspecies is a population of several bioty-
pes forming a more or less distinct regional facies
of a species.

Like »variety», the term »subspecies» has been used by taxono-
mists in most various senses. It has been used for any unit inter-
mediate between form and species, *i. e.* for morphologically distinct
groups of forms, for varieties in the sense defined above, for
sharply delimited populations considered to be too nearly related
to be raised to the rank of good species, for species of somewhat
dubious autonomy, or for distinct regional facies (geographical
races) of a species. The restriction of the term »subspecies» to
the sense last mentioned has been gradually inaugurated during
the last four decades, in the first line through the works of
WETTSTEIN (1896 *a*, *b*, 1898), K. JORDAN (1905), HARTERT (1910—1923),
SEMENOV-TIAN-SHANSKY (1910) etc., and now appears to be generally
accepted among zoologists, while botanists are still using the term
in a rather chaotic way.

Of other terms in use for the same concept, reference in first
line must be made to RENSCH's »geographische Rasse» (RENSCH
1929). As RENSCH restricts the species-concept to the species n o t
differentiated in regional facies, applying the term »Rassenkreis»
to all geographically differentiated species (comp. below p. 359),
he cannot use the term »subspecies» in our sense. Other synonyms
to our »subspecies» are KLEINSCHMIDT's »Form» or »Rasse» (comp.
below p. 359) and REICHENOW's (1904) »Konspecies» (comp. PLATE
1914 p. 134). By some authors the term »variety» has been used
either synonymous with our »subspecies» (comp. for instance
CRAMPTON 1917) or as a designation for subspecies of lower rank
(ENGLER 1916, comp. above p. 351).

Special reference must be made to the »ecotypes» described by
TURESSON (1922—1929). While in some cases they appear to be

identical with good species generally recognized by taxonomists, most of them may be regarded as s u b s p e c i e s in our sense (comp. RENSCH 1929 p. 78). In one of his later papers, TURESSON (1925 *b*) also applies the term »subspecies» to some of his earlier ecotypes. Theoretically, however, the ecotype-concept of TURESSON appears to be more comparable with the »subspecies oecologica» of ALPATOV (1922, 1923, 1924). ALPATOV pointed out, that several »subspecies geographicae» (= our subspecies) of a species often contained analogous »subspecies oecologicae», *e. g.* that quite analogous »subspecies oecologicae truncicolae» were found both in the European and in the Japanese subspecies of *Formica rufa*. In the same way, an »oecotypus campestris», »oecotypus arenarius» or »oecotypus salinus» in the sense of TURESSON (1925 *a* pp. 224—225) may be differentiated in more than one subspecies of a certain species. If the term »ecotype» could be restricted to such cases, it might be found useful to taxonomy, as it is obviously preferable to ALPATOV's term. As a synonym to our »subspecies» it appears to be of no use whatever.

That one f o r m may be found in several subspecies of one species, has been pointed out by several authors (comp. DOBRZAN-SKY 1924 p. 417). This means that it is not always possible to tell from an isolated specimen in a collection to which subspecies it belongs, if the locality of the specimen or the range of the subspecies is unknown (comp. SUMNER 1923 p. 239). Like varieties, subspecies are best described by a statistical survey of the forms constituting it (comp. CRAMPTON 1917, 1925 *a*, *b*). But unlike varieties, subspecies are conveniently named by Latin names, either after the pattern »*Pinus silvestris* subsp. *lapponica*» (*Pinus silvestris* *lapponica) or by a simple trinomial name like »*Pinus silvestris lapponica*». The latter method is generally accepted by present zoologists and by some American botanists (comp. for instance HALL and CLEMENTS 1923, BABCOCK and HALL 1924, HALL 1928); it appears to be practical enough to be accepted also by botanists in other countries.

Unlike the species, subspecies are neither sharply delimited from each other nor connected by transitional populations of the »hybrid»-type (comp. below p. 391). The various subspecies of a species are continuously intergrading into each other, their delimitation thus being infinitely much more arbitrary than that of the species. Still there may be more or less distinct zones with increased change in the composition of a species-population, which

of course must be carefully taken into account at the delimitation of the subspecies.

A multitude of good examples of the differentiation of animal species into subspecies is given by RENSCH (1929). Wellknown examples from the vegetable kingdom are the subspecies of *Pinus silvestris* (*lapponica, septentrionalis, borussica, scotica, engadinensis* etc., comp. for instance SCHOTT 1907, SYLVÉN 1916 *a, b,* CAJANDER 1921), and of *Picea excelsa* (the eastern subspecies of which is often treated as a separate species under the name of *Picea obovata,* but according to CAJANDER *l. c.* continuously intergrades into the European subspecies). Many alpine plant-species are found as different subspecies in different parts of the European Alps (*e. g. Silene acaulis* and several species of *Saxifraga,* comp. ENGLER 1916). An analogous differentiation in subspecies is found in many alpine and subalpine plant-species of the Southern Alps of New Zealand, a good example being furnished by *Celmisia petiolata* Hook. f. Of this species, which plays a prominent rôle in a good part of the mountain-chain, I had the opportunity of examining at least three different subspecies in the field (one in the upper Waimakariri region at about lat. 43°, one in the Mount Cook region at about lat. 43° 40′ and one in the Routeburn-Humboldt Mts region at the western end of Lake Wakatipu at about lat. 44° 40′). Each of those subspecies was composed by a large number of forms, the general composition of the population appearing to change gradually from the northernmost subspecies of the Waimakariri region to the southernmost one of the Northern Fiord District, which may or may not be connected with *Celmisia verbascifolia* of the Southern Fiord District by a gradual transition.[1] — In many (but by no means in all)

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[1] In the Waimakariri-population (on Hills Peak N. of Arthur's Pass and Mt Misery near Cass, both visited by me in the company of Dr. H. H. ALLAN), I saw only forms with distinctly petiolate, rednerved and more or less serrulate leaves with rounded base, in the Wakatipu-population (on Bold Peak, Lake Harris Saddle, and the peaks around the latter, visited by me partly in the company of Mssrs G. SIMPSON and J. S. THOMSON) only forms without distinct petiolae, with leaves gradually attenuated at the base, not serrulate, or very indistinctly, and with the nerve either green or red. The Mt Cook-population (on Sealey Range) distinctly kept in the middle between those two extremes, consisting partly of unpetiolate, partly of more or less petiolate forms, with the nerve red or green and more or less indistinct serrulation. Some of the forms in the Wakatipu-population are very much approaching *C. verbascifolia* Hook. f., and have even been referred to this species by CHEESEMAN and COCKAYNE (some of my specimens Dr. COCKAYNE named

New Zealand plant genera the differentiation has led to a large number of sharply delimited alpine and subalpine species with comparatively small distribution areas and no distinct differentiation of subspecies, while the species of the lower belts are more widely distributed and often (but not always) differentiated into a number of continuously intergrading subspecies. The explanation certainly must be sought for in the lack of effective barriers in the lower belts, while in the alpine and subalpine belts a certain amount of isolation is often brought about by broad valleys etc. A good example is furnished by the genus *Hebe*, the most common lowland-species *Hebe salicifolia* being distributed throughout New Zealand but differentiated in several subspecies (comp. COCKAYNE and ALLAN 1926 *a* pp. 17—19, 1927 p. 274), while most mountain-species show comparatively small distribution areas and no distinct differentiation of subspecies.

10. **The species.**

The smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes, are called species.
A species thus is a population consisting either of one strictly asexual and vital biotype, or of

»C. verbascifolia var. *pubescens»*). However, what I have seen of the latter species (I studied it in the field on Wilmot Pass and Mt Barber at lat. 45° 30′ together with Mr. W. R. B. OLIVER) is constantly more glabrous than the most glabrous individuals that I brought home from the Wakatipu-population. In the Dominion Museum at Wellington, where D. PETRIE's large collections are preserved, I saw forms of *C. verbascifolia* closely resembling my own from Wilmot Pass and Mt Barber, collected as far north as in the Clinton Valley (lat. 44°50′), while all the specimens collected further north or further east in the Fiord and South Otago Districts far more resembled those of my Wakatipu-population. Further field-studies must decide whether *C. verbascifolia* and the southern subspecies of *C. petiolata* are connected only by a narrow hybrid-zone (to which then probably some of the forms in my Wakatipu-population should be referred) or by a broad zone of more continuous intergrading. In the latter case it may prove necessary to include *C. petiolata* and *C. verbascifolia* into one heterofacial species. However, it must be pointed out that my knowledge of the populations concerned is far too incomplete to guarantee that not further field-studies will reveal zones of discontinuity even within the huge population here referred to *C. petiolata,* enabling future taxonomists to split it into several species — though what I have seen of it appears to make this rather improbable.

a group of practically undistinguishable, strictly asexual and vital biotypes, or of many sexually propagating biotypes forming a syngameon[1] separated from all others by more or less complete sexual isolation or by comparatively small transitional populations.

One of the greatest difficulties confronting every attempt to give a generally applicable species-definition is formed by the fundamental difference between the constitution of sexual and asexual populations. Owing to this difference, different alternatives for sexual and asexual populations are necessary in the general definition of the species-concept. While there is a comparatively good agreement (at least theoretically) among present-day botanists regarding the species-concept in sexual populations, very different opinions are found regarding what should be called species in asexual populations. Many geneticists find it absurd to call single asexual biotypes or even small groups of practically undistinguishable asexual biotypes species, when most sexual species contain an enormous number of biotypes (comp. for instance TURESSON 1922 p. 232, 1923 p. 173, 1926 b pp. 187—190, 203, 1929 a, CLAUSEN 1922, TEDIN 1925 pp. 355—356) — but as yet they have failed to tell what unit in asexual populations should be better corresponding to the sexual species. The definition recently given by TURESSON for his new concept »agamospecies» (1929 a pp. 332—333: »An apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having common origin») is obviously too vague to be of any practical value at all, as it is equally applicable to any unit of higher rank than the biotypes in the genera concerned (from a group of a few biotypes up to the whole genus!). As K. JOHANSSON (1927) has pointed out for the *Hieracia Vulgata*, it is often a rather hopeless task to group the apomictic »microspecies» to higher units of any taxonomical importance to which the name »species» could be applied. Thus in those cases we simply have to apply the species-concept to the »microspecies», if we wish to use it at all in the genera concerned. The claim of certain geneticists that the species-concept should be applied to units of about the same size and the same polymorphy, will hardly be generally accepted by taxo-

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[1] = »intercrossing population». Comp. LOTSY 1918, 1919 a, b, 1921, DANSER 1924 pp. 204—209.

nomists, though the same view is sometimes found also among taxonomists (comp. below). Among most present-day taxonomists the view is firmly established, that a natural species-concept can be founded only upon the principle of d i s c o n t i n u i t y, *i. e.* that we have to delimit our species simply after the lines or zones of discontinuity found in nature, without any prejudice as to the convenient size of the species. If Nature has made some species larger and more polymorphic than others, we simply have to accept this arrangement.

Far more difficult than the delimitation of species in strictly asexual populations (which in spite of the often very great number of species probably is one of the easiest tasks confronting the taxonomist) is the dealing with f a c u l t a t i v e l y asexual populations. As mentioned above (p. 344) the stability and permanency of the clones in such cases is often hardly sufficient to give them the rank of species, and the species-delimitation in facultatively asexual populations may certainly be a most difficult task (comp. for instance the genera *Rubus* and *Rosa*). Similar difficulties are met with in facultatively autogamous populations (regarding the delimitation of species in those comp. SHULL 1923, 1929 *a, b*).

As was mentioned above, the acceptance of d i s c o n t i n u i t y as the only base for the delimitation of species must lead to the rejection of s i z e as a base for that delimitation. There is a rather widespread tendency among present-day biologists (especially among zoologists) to apply the term »species» only to populations of comparatively equal size (comp. for instance RYDBERG 1929 and the authors mentioned below). A consequence of this tendency is the method of certain modern zoologists to restrict the use of the term »species» to comparatively homogenous populations not differentiated into distinct geographical facies, substituting it with the term »Rassenkreis» (RENSCH 1926, 1929, preceded by the »typus polymorphus» of ENGLER 1872, 1916, the »Rassenkette» of F. and P. SARASIN 1899, and the »Formenkreis» of KLEINSCHMIDT 1901 — 1926) when dealing with more heterogenous populations (species in our sense) differentiated in »geographische Rassen» (= our subspecies, comp. above p. 354). RENSCH is perfectly right in pointing out that his »Arten», as regards size and polymorphy, are far more corresponding to the »geographische Rassen» than to the »Rassenkreise». But if we accept d i s c o n t i n u i t y, not size nor polymorphy, as the only base for the delimitation of

species, both RENSCH's »Arten» and his »Rassenkreise» must be included in the same species-concept and carry the name of species.

The rejection of the principle of size and polymorphy as a base for the delimitation of species also implies the rejection of the widespread belief that species should be delimited after »the magnitude of the differences» between the forms concerned.[1] According to the species-concept defined above, two forms may be very different and still belong to the same species, if connected by transitional forms, while two other forms may be much less different and still belong to two different species. •

In recent genetical literature we often find the term »species» substituted by »Linnean species» or »Linneon» (the latter term proposed by LOTSY 1916). The necessity or even desirability of those new terms is difficult to realize. LOTSY's invention of the term »Linneon» was made necessary simply by his radical proposition to apply the term »species» in a quite new sense, namely as a designation for homozygous biotypes (comp. above p. 341). The latter proposition was declined by practically all biologists, but nevertheless the new term »Linneon» has been accepted by many. If the term »species» is kept in its old sense, »Linneon» in the sense of LOTSY of course is completely superfluous. — COCKAYNE and ALLAN (1927, comp. also COCKAYNE 1928 p. 7, 1929 p. 23) have proposed to use »Linneon» in a modified sense, *i. e.* for a unit superior to the species, or for two or more closely related species connected by hybrids and confused by earlier taxonomists. Against this use of the term may be advanced not only the confusion easily resulting from the use of the same term in two different senses, but also that it appears to give a somewhat wrong idea of what the species of LINNÆUS really were. Surely many of the species described by LINNÆUS on the base of bad and insufficient herbarium-material from foreign countries were aggregates of several good species in our sense (*i. e.* Linneons in the sense of COCKAYNE and ALLAN) — but in the flora studied by LINNÆUS in the field most of them certainly

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[1] As I have myself been accused of having advocated this principle by TURESSON (1925 *a* p. 232), it may be appropriate to point out that TURESSON's accusal is based simply upon a wrong citation of my criticized paper, namely by a translation of »scharf genug abgegrenzt» and »scharf abgesondert» into »sufficiently different».

were just identical with the species of present day taxonomists (or in some cases even with units of still lower rank!). There are also examples of Linnean species (in the true sense, namely species described by LINNÆUS) that were degraded to forms by later taxonomists and reestablished as species first by the modern monographers of the genera concerned (*e. g. Poa angustifolia*).

Also the terms »ecospecies» and »coenospecies» recently proposed by TURESSON (1929 *a*) appear to be easily dispensable. TURESSON's »ecospecies» is practically only another synonym for our »species», if the asexual species (and some very dubious sexual species with prevailing autogamy) are excepted. His »coenospecies», which according to the definition should consist of species having »a common origin so far as morphological, cytological or experimental facts indicate such an origin», are examplified partly by the dubious species *Capsella bursa pastoris* and *Erophila verna* (both with prevailing, but not obligate, autogamy), partly by groups of nearly related and frequently hybridizing allogamous species (*Viola tricolor* and *V. arvensis, Geum rivale* and *G. urbanum, Salix caprea* and *S. viminalis*, comp. also the practical application of the term in the latter sense in the genus *Galeopsis* by MÜNZING 1930). According to TURESSON's definition any taxonomical unit superior to the species may be called a coenospecies. If any new terms are needed for the lowest of those units, I prefer DANSER's more definite terms »commiscuum» and »comparium» (comp. below pp. 387 and 398).

The distinction between »simple» and »compound» species recently proposed by COCKAYNE and ALLAN (1927) certainly is very useful, though it may well be discussed which species are really worthy of being called »simple». According to COCKAYNE and ALLAN (1927 pp. 259—260, comp. also COCKAYNE 1928 p. 7, 1929 p. 22) a simple species is a species that contains only one »jordanon» (comp. above p. 350), while a compound species is made up of two or more jordanons. But even in the simplest sexual species certainly intensive analyses will reveal a very great number of slightly differing forms, and in strictly allogamous species even every individual probably represents its own biotype (comp. above p. 340). Thus the only strictly simple species existing would be those consisting of a single strictly asexual biotype, while all other species would be more or less compound.

As the species-concept is taken in this paper, it is necessary to distinguish at least four main types of species:

1. **Asexual species** (species consisting of one or several strictly asexual biotypes).

   a. S i m p l e   a s e x u a l   s p e c i e s (species consisting of one strictly asexual biotype). To this type probably many apomictic species of *Hieracium* sect. *Vulgata, Taraxacum*, etc., in first line those with very small distribution-areas, must be referred, and possibly also a part of the lichen-species never developing apothecia but constantly propagated by soredia, isidia, or undifferentiated thallus-fragments (comp. above p. 345).

   b. C o m p o u n d   a s e x u a l   s p e c i e s (species consisting of several, practically indistinguishable, strictly asexual biotypes). To this type belong probably many of the apomictic species of *Alchemilla*, many of the more widely distributed apomictic species of *Taraxacum* and *Hieracium* sect. *Vulgata*, and many of the asexual lichen-species mentioned above.

   As has been pointed out by SAMUELSSON (1922) and K. JOHANSSON (1927), many of these apomictic species in *Alchemilla, Hieracium, Taraxacum* etc. were recognized by taxonomists long before the discovery of apomixis in the genera concerned. Quite independently of the interesting explanation furnished by the apomixis, they were thus recognized in the field as natural, sharply delimited units analogous with other species. Certainly it would involve a good bit of absurdity, if, following the advise of certain modern geneticists, we would take the discovery of their apomixis as sufficient reason to reduce them to units of lower rank than that previously given to them on the base of unprejudiced field-studies.

2. **Sexual species** (species consisting of a great number of freely intercrossing — or partly autogamous — biotypes).

   a. H o m o f a c i a l   s e x u a l   s p e c i e s (»Arten» *sensu* RENSCH). Regionally undifferentiated, *i. e.* consisting of only one regional facies (subspecies).

   b. H e t e r o f a c i a l   s e x u a l   s p e c i e s (»Rassenkreise» *sensu* RENSCH). Regionally differentiated, *i. e.* differentiated into several regional facies (subspecies).

   As a close survey will probably reveal local facies (varieties) also in most species of the first of those groups (at least in those with more or less stationary individuals), the term »homofacial» is not quite adequate — but as I have not been able to find out any better term, it may

be used at least provisionally. Many homofacial sexual species give the impression of a »simple species» *sensu* COCKAYNE and ALLAN, as they consist of biotypes differing only very slightly from each other. But many would be referred to COCKAYNE's and ALLAN's »compound species», obviously containing biotypes differing enough from each other to be easily recognized as different forms. This will be the case even in many highly inbred species with very small distribution-areas. In *Gentiana antipoda*, for instance, endemic in Antipodes Island, one anthocyaninic and one non-anthocyaninic form are easily recognized, (KIRK 1895), and I found just the same in *G. antarctica*, endemic in Campbell Island.

Examples of heterofacial sexual species are given above under the subspecies (pp. 356—357). Of course they all belong to COCKAYNE's and ALLAN's type »compound species».

As was mentioned above already in the definition of the species, the limits of sexual species may be of different kinds. While some species are separated from each other by complete sexual isolation, others are connected by (comparatively small) transitional populations of various kinds (hybrids). It appears most convenient to discuss those two kinds of species-limits separately.

I. Species separated from each other by complete sexual isolation.

The limits between such species may be said to form distinct l i n e s o f d i s c o n t i n u i t y in the series of biotypes. They may be formed either by geographical or by merely physiological isolation. In the former case, the species concerned may be perfectly fertile with each other when brought together in an artificial way (comp. DANSER 1929 *b* p. 425), or the geographical isolation may be guarded also by physiological isolation, *i. e.* by an inherent unability of the individuals from one species to cross with individuals from the other. In the latter case (*i. e.*, when there is no geographical isolation but only physiological isolation of species growing together in the same area), isolation may be due to any of the following causes. 1. Differences in the breeding (or flowering) season or breeding places (the latter only in animals, comp. PLATE 1913 pp. 527—531, ROBSON 1928 pp. 122—124). 2. Morphological, physiological or — in animals — psychological unability of the individuals of one species to cross with those of the other species (comp. ROMANES 1886, 1897, GULICK 1872—1905,

PLATE 1913 pp. 531—549, ROBSON 1928 pp. 122—130). 3. Anyone of the two most severe types of »diplontic sterility» described by MÜNZING (1930 p. 318), *i. e.*, the dying of the diplont at the zygote or embryo stage, or the incapability of the seedlings of an independent existence.

In cases of purely geographical isolation it is often extremely difficult to decide whether the isolated populations should be treated as separate species or as mere parts of the same species. Here four different cases must be discussed separately.

1. If all the individuals of one population differ both greatly and constantly from those of the others, everybody will agree that the two populations represent different species. Thus everybody who has studied the Gentians of the subantarctic islands of New Zealand will agree that *Gentiana antipoda* of Antipodes Island, *G. antarctica* of Campbell Island, and *G. cerina* of the Auckland Islands (of which *G. concinna* of the same islands probably is only a form, comp. KIRK 1895) are good species, though clearly representing one natural group (series) of vicarious species (»Artenkreis» *sensu* RENSCH).

2. If all individuals of one population differ constantly but very slightly from those of the others, many taxonomists will treat the two populations as parts (subspecies or varieties) of one species, while others (and among them myself) will keep them apart as separate species. According to the literature, such a case appears to be represented by the middle-european *Pinus cembra* and the Northeast-European and West-Siberian *Pinus sibirica,* by many authors (and also by myself in a previous paper, comp. DU RIETZ 1930 pp. 320—321) treated as mere subspecies or even as varieties of one species. Other cases are commonly found in species isolated in the different islands of one island-group (comp. RENSCH 1929 p. 100 etc.) or in the different mountain-massifs of one mountain-chain. A good example is furnished by *Pleurophyllum Hookeri* (Compositae) in the subantarctic islands of New Zealand, by previous authors regarded as one species occurring in identical forms in the various islands, but according to my own observations in the field (in the Auckland and Campbell Islands, supplied with studies of herbarium-material from those islands and Macquarie Island) represented by slightly but probably constantly differing populations (= species) in those three island-groups.

3. If the average composition of one population is distinctly

different from that of the others, but certain biotypes from one population so closely resemble biotypes from the others that they must be referred to the same forms, most taxonomists will probably agree that the populations do n o t represent different species, but mere subspecies of the same one. Theoretically, the opposite opinion would be quite possible to defend, but practically it appears imperative to delimit species in such a way that it is possible to determine any well-developed individual also without knowing its provenance. At present I am not able to demonstrate any botanical example of the case concerned — the average composition has been properly investigated in very few plant-species — but a very good zoological example is afforded by CRAMPTON's (1925 *b*) thorough analysis of the *Partula gibba*-population of the two Mariana-islands Guam and Saipan.

4. If the two populations differ only slightly in average composition, nobody of course would think of treating them as different species or even subspecies, in spite of their isolation from each other.

II. Species connected with each other by transitional hybrid-populations.

In this case the limits between the species may be said to form not lines but z o n e s o f d i s c o n t i n u i t y in the series of biotypes. Those zones may be of several different types.

1. The transitional hybrid-population consists of merely sterile individuals.

This type of transitional hybrid-populations is certainly very common, and very many examples are described in botanical and zoological literature. The sterility may be of many different degrees. In extreme cases, leading over to the two severest types of diplontic sterility mentioned above (p. 364), no reproductive organs at all are formed, though the vegetative development may be quite normal. Examples of this subtype are mentioned by FOCKE (1881 p. 477: some hybrids of *Rhododendron*, *Epilobium*, *Cereus* and *Hymenocallis*), HERIBERT-NILSSON (1918: *Salix viminalis* × *fragilis*), and MÜNZING (1930 pp. 318—319). To the same subtype possibly belong the following New Zealand *Celmisia*-hybrids, of which I only succeeded to find non-flowering individuals (I do not

know whether they have been found flowering by my New Zealand colleagues, to which they are probably all well-known, though little has been published about them yet): *Celmisia coriacea × Lyallii* (mentioned already by COCKAYNE 1923 and 1925, found by myself in several individuals on Sealey Range in the Mt Cook region and on Bold Peak in the Humboldt Mts[1]), *C. coriacea × Petriei* (Bold Peak, only one individual), *C. Lyallii × petiolata* (Sealey Range in several individuals), *C. petiolata × Petriei* (Lake Harris Saddle, only one individual), and *C. petiolata × sessiliflora* (on the ridge S. of Lake Harris Saddle, only two leaf-rosettes). The same may be the case with the remarkable hybrid *Olearia Crosby-Smithiana × ilicifolia*, at the time of my New Zealand visit known only in a single and — as far as I know — non-flowering shrub at Wilmot Pass in the Fiord District (discovered by Mr. LESLIE MURRILL, who brought Mr. W. R. B. OLIVER and me some branches during our excursion to Doubtful Sound).

Another subtype is represented by the hybrids in which reproductive organs are developed but more or less defective, either morphologically or only physiologically (comp. MÜNZING 1930 pp. 314—322). The sterility of many hybrids has been well known since very long ago (comp. FOCKE 1881 p. 477 and ROBERTS 1929), and from time to time even the theory has been advanced that all true »species hybrids» should be at least more or less sterile. Thus the investigation of the seed-production and of the quality of the pollen has become a well-established method in taxonomy for the testing of supposed hybrids. Abundant examples of sterile hybrids are easily found in botanical (and zoological) literature (comp. for instance FOCKE 1881, KERNER 1898, DE VRIES 1903, MÜNZING 1930, and modern floristical handbooks, especially those of Scandinavian countries). A very interesting account of the hybrids in the section *Lapathum* of the genus *Rumex* is given by DANSER (1924); some of those hybrids are completely sterile, while others are nearly sterile, producing only very few germinable seeds (comp. below p. 368). As to the New Zealand flora, I do not know any hybrids of this subtype with certainty (comp. COCKAYNE 1929 p. 11), but there is little reason to doubt that it is common there too, though not as well known yet as fertile and highly polymorphic hybrids. — As mentioned by MÜNZING (l. c.),

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[1] On Bold Peak my *Celmisia*-studies were made in company with Mssrs G. SIMPSON and J. S. THOMSON.

there are many degrees even of complete sterility in hybrids, from types with the flowers degenerating already in the bud-stage to types with flowers of quite normal appearance, but with no seed-production. In the latter case, according to Münzing, either diplontic or haplontic sterility may be responsible.

Hybrids consisting of perfectly sterile individuals are always fairly homogenous, though some polymorphy may be brought about by intraspecific differences between biotypes involved in the interspecific crosses. They do not, as a rule, play any considerable rôle in nature, and do not considerably disturb the sharp limits of the species concerned.

2. The transitional hybrid-population consists of more or less fertile individuals.

The existence of more or less fertile hybrids has been well known, though often doubted, since the time of Kölreuter (1761, comp. Kerner 1871 pp. 34—35). Focke (1881 p. 477) enumerates quite a lot of genera in which fertile hybrids are more common than sterile ones. The considerable polymorphy of many of those fertile hybrids was also well known (comp. Focke l. c.). Still it is first in recent years that highly polymorphic hybrids have come to their full right in the discussion of the species-problem.

Also in this type of transitional hybrid-populations two subtypes may be distinguished. In the first subtype the transitional hybrid-population is obviously less vital than the two species-populations concerned, while in the second subtype the hybrid-population exhibits a vitality quite comparable with that of those species-populations.

In the first subtype of fertile hybrid-populations, comprising those with a vitality clearly lower than that of the species concerned, the hybrid-population may obscure the limit between the two species only rather· slightly, as the hybrid-population will play a rather modest rôle in nature compared with that of the two species-populations, and will not be able to enter into serious competition with them in any habitat. The lack of vitality in the hybrid-population may be due to several causes. Though not completely sterile, the biotypes of the hybrid-population may in many cases exhibit a rather low fertility. Both in those cases and in the cases of full fertility the vitality of the hybrid-individuals may be too low to enable them to compete successfully with the species.

Some boreal examples of hybrids of this subtype may first be mentioned. According to HERIBERT-NILSSON (1918), the hybrid between *Salix caprea* and *S. viminalis* cannot in spite of its fertility compete with the parent species, owing partly to certation phenomena, and partly to characters lowering the vitality in various ways. Many of the *Salix*-hybrids found in the indigenous vegetation of Sweden obviously belong to the same type. — In the hybrid *Viola arvensis* × *tricolor* according to CLAUSEN (1926) there are no biotypes able to compete successfully with the parent species, neither in experimental plots nor in nature. — Similar cases are found in some of the hybrids of *Rumex* sect. *Lapathum, e. g.* in *Rumex aquaticus* × *hydrolapathum* (*R. maximus*, comp. DANSER 1924 pp. 186—188). Here fertility is always much lower than in the parent species, and the hybrids have therefore no chance in the competition with those species. — Just the same, according to E. ANDERSON (1928) is the case in the North American hybrid *Iris versicolor* × *virginica.*

Analogous cases are easily found in the flora of New Zealand. Among the best examples are those provided by the hybrids *Ranunculus Buchananii* × *Lyallii* (*R. Matthewsii* Cheesem., comp. COCKAYNE 1921 p. 359, 1923 p. 118, 1925 p. 63, 1928 p. 240, ALLAN 1926 *c* p. 534) and *Ranunculus Buchananii* × *Simpsonii* (comp. COCKAYNE 1928 pp. 241, 301, 302) both of which I have had excellent opportunities to study in the field in the upper Routeburn Valley in the Fiord District of South Island (in the company of Mssrs G. SIMPSON and J. S. THOMSON). *Ranunculus Lyallii* is an important dominant of the s u b a l p i n e meadows throughout the wet mountains of the southern and middle parts of South Island, *R. Buchananii* forms small meadow-fragments in wet rock-crevices, rock-ledges, rock-slides etc. in the a l p i n e belt of the Fiord and South Otago Districts[1] only, and *R. Simpsonii*[2] is one of the most

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[1] As to the Botanical Districts of New Zealand comp. COCKAYNE 1928.

[2] Possibly *R. Simpsonii* Ckn and Allan (1926 *b* p. 58) will turn out to be better treated as a subspecies of *R. sericophyllus* Hook. f. (Western District), with which it was united by CHEESEMAN (1925 p. 444) and which it replaces in the Fiord District. On Sealey Range in the Mount Cook region, where *R. sericophyllus* is abundant, I found a continuous series of biotypes connecting the typical villose forms with nearly glabrous forms indistinguishable from the true *R. Simpsonii* of the Fiord District. Further field-studies by New Zealand botanists must decide whether there is a comparatively narrow hybrid-zone between the pure *R. sericophyllus* - population of the north and the pure *R. Simpsonii* - population of the

important dominants of the open chionophyte-meadows[1] in the alpine belt of the Fiord District. *R. Buchananii* and *R. Lyallii* frequently meet on steep slopes along the alpine-subalpine border in the Fiord District, and in those places the highly polymorphic hybrid is found, forming a very fine series of transitional forms connecting the two species. In my rather rich collection of hybrid-specimens, the development of the pollen varies from individuals with n e a r l y all pollen-grains normally developed to such with more than 50 % shrivelled. In one specimen a great reduction of the seed-production was observed, not 50 % — and in some flowers much less — of the achenes being fertile; if this is the rule or not I do not know. I never saw the hybrid dominating. Even in the transitional belt the hybrid obviously has no chance in competition with the two species. — This is still more the case with the hybrid *R. Buchananii* × *Simpsonii*. Though those species are frequently growing quite near each other in the alpine belt (they are even frequently met together in the same community), the hybrid was found only in one place, namely on a large wet shingle-slip suitable for both species. The hybrid was very polymorphic, connecting the two species by a series of transitional forms; four extravagant individuals with more or less transformed petals were found. The pollen was bad: in many specimens nearly all pollen-grains were shrivelled, while in others nearly 50 % (but not more) could be normally developed. Though a good number of individuals of the hybrid were found (growing among the mixed parent species), it was quite obvious that it had no chance at all in the competition.

None of those two *Ranunculus*-hybrids can be said to disturb the delimitation of the species in any considerable way. The hybrid-individuals are quite easy to pick out, and compared with the large populations formed by the pure species they play a very insignificant rôle in nature.

south, in which case the two populations must be kept as species, or a more continuous transition, in which case they would be better treated as subspecies of one species (comp. above pp. 356—357).

[1] *Chionophytes* (from χιων = snow) are plants dependant of a very long snow-covering (= »Schneebodenpflanzen» in German). According to their relation to the length of the snow-covering (certainly one of the most important ecological factors in the alpine belt of all mountains) the alpine plant-communities may be divided into four groups: *chionophilous, subchionophilous, subchionophobous* and *chionophobous*.

In the New Zealand species of *Nothofagus* perhaps still better examples of this subtype of species-limits are found. *Nothofagus Solandri* and *N. truncata* have about the same main distribution-area in the *Beilschmiedia tawa*-belt of New Zealand (= the lower parts of North Island, except in the extreme north, and northernmost South Island), and to a large extent form mixed forests, but nevertheless the hybrid between those two species is only found in single individuals or a few trees side by side. Though the hybrid is highly polymorphic and evidently more or less fertile, forming a series of transitional forms connecting the two species, its vitality and power of competition are apparently so inferior to those of the two species, that the species can stand out as sharply delimited units even when growing together in the same forest, *e. g.* in the beech-forests near Wellington, where Dr. L. COCKAYNE and Mr. E. ATKINSON kindly introduced me to this hybrid (comp. COCKAYNE and ATKINSON 1926, COCKAYNE 1926 and 1929, COCKAYNE and PHILLIPS TURNER 1928.) — The hybrid *Nothofogus cliffortioides* × *fusca* is evidently more vital. It is common in the mixed *N. cliffortioides-fusca*-forest of South Island, is obviously quite fertile and exhibits an extreme polymorphy (COCK-AYNE 1923, 1926, 1929, COCKAYNE and ATKINSON 1926, COCKAYNE and PHILLIPS TURNER 1928). »Generally in *Nothofagus cliffortioides-fusca* forest, hybrids form a very small percentage of the trees, but perhaps 5—10 per cent occur with fair frequency. In some places, however, there may be at least 50 per cent of hybrids, but such spots are small in extent. Nevertheless, it is clear that the hybrids can well hold their own, a statement substantiated by the presence of hybrid seedlings in great numbers beneath hybrid trees. After a forest fire hybrids may occur in great profusion and the reinstated forest will certainly contain more hybrid trees than did the former community» (COCKAYNE 1929 p. 14). Still even this hybrid is not vital enough to prevent the two species from standing out as quite distinct units. When studying it in the Dart Valley and at Kinloch (W. end of Lake Wakatipu) I got the impression that the remarkable frequency of the hybrid in y o u n g forest mentioned by COCKAYNE and easily observed at Kinloch was only ephemeral, the vast majority of those young hybrid-individuals getting lost in the long run in competition with the parent species. In the mature *Nothofagus*-forest there is room only for quite few of the trees of the young forest, and in this

final tree-layer of giant *Nothofagus*-trees the hybrid-trees appear to have small chances to get a place. In old, mature *Nothofagus cliffortioides-fusca*-forest I never found more than single individuals of the hybrid. If the habitat is suitable for *N. fusca*, which is much more pretentious than *N. cliffortioides*, even the latter species appears to have small chances to survive in the very old forest.

In the second subtype of fertile hybrid-populations, comprising those with the vitality of the hybrid-population equalling that of the species concerned, we meet the most difficult cases of species-delimitation that may confront a taxonomist. In those cases, the species are saved from being completely swamped only by occupying different distribution-areas or at least different habitats in the same distribution-area. In the areas (or habitats) where they meet, they fleet together into one vast syngameon, the greater part of which may clearly belong to the hybrid. If this hybrid-area is m u c h smaller than the areas occupied by the pure species-populations, the species may still stand out as quite distinct units. But if the hybrid-population is of a size comparable with that of the pure species-populations, the taxonomical treatment of the populations is extremely difficult. And still worse is the case when the hybrid-population tends to outnumber the pure species. But as long as s o m e areas of considerable size are occupied by the pure species, there is still a possibility left to keep the species distinct, though in all those cases the question may arise whether it would not be a better method to treat the two species and the hybrid only as different subspecies of one heterofacial species. It is in those cases that pure herbarium-taxonomy proves to be utterly unable to solve the problems (and pure garden-genetics too!), and that the necessity of a g e o g r a p h i c a l f i e l d - m e-t h o d will stand out in the most imperative way.

It is often rather difficult to decide whether a certain hybrid should be referred to this or to the preceding subtype. This is especially the case when the species concerned occupy only different habitats in the same distribution-area. In the hybrid *Geum rivale* × *urbanum*, for instance, it appears to be somewhat doubtful whether the comparatively small rôle played by the hybrid in nature is due partly to fertility- and vitality-factors (ALMQUIST 1926 pp. 67—68, TURESSON 1929 *a* p. 329) or only to the differences between the habitats of the two species and the

supposed scarcity of intermediate habitats (WINGE 1926 *b* p. 594) combined with complex heredity of certain groups of characters (WINGE 1928 p. 231). In the following discussion, however, I will try to choose such examples where little doubt is possible regarding the full fertility and vitality of the hybrids.

Let us begin then with some examples of species forming hybrids with full fertility and vitality, but still kept distinct by the adaptation of the two species to different habitats in the same main distribution-area.

The example of such species most frequently met with in genetical literature is the species-pair *Melandrium album* (*Melandrium pratense, Lychnis diurna*) and *M. rubrum* (*M. silvestre, Lychnis vespertina*). While geneticists of the purely experimental garden-school may fail to recognize those two species as natural units, owing to the full fertility and vitality of the hybrid (comp. SHULL 1923), field-working taxonomists (and geneticists combining the experimental garden-work with comparative field-studies) find little or no difficulty in keeping the two species distinct. In the areas where both species occur, they occupy so different habitats that the hybrid cannot play any considerable rôle compared with the pure species (comp. HAGEDOORN 1921 pp. 132—134). In Sweden only *M. rubrum* belongs to the indigenous vegetation, being common in somewhat wet forests of the meadow-type in most parts of the country, and extending even into the open meadows of the low-alpine belt (according to TURESSON 1925 *a* pp. 184—189 it is differentiated in four more or less distinct »ecotypes» or subspecies). *M. album* here is an introduced weed hardly entering the indigenous plant-communities. According to ALMQUIST (1926 pp. 66—67), the hybrid is especially common in cultivated fields in some parts of North Sweden, but it may be found everywhere where the two species grow near each other. It does not enter the indigenous plant-communities, and the wild *M. rubrum* - population mostly keeps quite pure.

A good example of species occupying so different habitats within the same area that the limit between them is kept distinct in spite of the vitality of the hybrid, is afforded by *Salix herbacea* and *Salix lapponum* in the mountains of Scandinavia. *Salix lapponum* is one of the dominants of the willow-scrub covering much of the moist ground in the low-alpine belt, while *S. herbacea* is a minute dwarf-shrub or even hemicyptophyte,

being one of the most important dominants of the middle-alpine and high-alpine belts (comp. Du RIETZ 1930 p. 354), but in the low-alpine belt playing a rôle only in the extreme chionophyte-communities. The hybrid is quite fertile and exhibits a remarkable polymorphy, connecting those so different species by a series of forms (comp. FLODERUS 1909 pp. 25—27). It may be found wherever the species meet, and is mostly quite common especially along streams in the low-alpine belt. According to FLODERUS (l. c.) it may occasionally even »be so abundant that it forms large continuous mats lying so close to each other that they give a dominating character to the vegetation-picture». But this is only in especially favourable districts where there are large tracts of country belonging to the low-middle-alpine transition-belt. The vast majority of the *Salix herbacea-* and *S. lapponum -* populations are kept comparatively isolated from any chance of hybridizing with each other, and compared with those immense pure populations, the hybrid plays such a small rôle in nature that nobody would think of uniting *S. herbacea* and *S. lapponum* to one species or even considering the limit between them as »bad».

Analogous cases are easily found in the flora of New Zealand. One of the best examples is certainly that formed by *Dracophyllum filifolium* and *D. recurvum* (OLIVER 1928, ALLAN 1928), which I had splendid opportunities to study on Mount Conspicuous in the Ruahine Range (under the guidance of Dr. H. H. ALLAN) and especially on Ruapehu (in the central part of North Island). Both species have their main distribution-area in the subalpine belt of the central mountains of North Island, though the area of *D. recurvum* extends to Hikurangi in the East Cape District and that of *D. filifolium* to Mt Egmont and to Cook Strait. *D. filifolium* is one of the dominants of the closed subalpine scrub, while *D. recurvum* is one of the two leading dominants of the open dwarf-shrub heath covering most of the wind-exposed ridges. In its typical state the latter species is a prostrate dwarf-shrub, while the former is an erect shrub. They are connected by a hybrid consisting of a most polymorphic series of forms and, if I may rely upon my own observations on Ruapehu, these exhibit a vitality fully equal to that of the pure species. In the dwarf-shrub heath of the wind-exposed ridges *D. recurvum* keeps pure, as *D. filifolium* does mostly in the closed scrub (though not to the same high degree), but in the open tall tussock (*Danthonia Raoulii*) vegetation

dotted with low shrubs the two species meet, and there the limit between them is completely smoothed out by the hybrid in its innumerable forms, mostly quite outnumbering the pure species. As much of this open tussock-country may be due to fire, the rôle played by the hybrid has possibly increased in comparatively recent years.

Another similar example is found in the same genus, namely the species-pair *Dracophyllum Oliveri*[1] and *D. prostratum,* both occurring on more or less boggy ground in the South Otago and

[1] Under this name I propose to raise OLIVER's »*Dracophyllum longifolium* f. 3» (OLIVER 1928 p. 702) to the rank of a species. Though OLIVER is pointing out the compound character of his (and previous authors') *D. longifolium,* he provisionally keeps it as one species, dividing it into three forms only. As far as my experience goes, those three forms are quite as good and definite units as many *Dracophyllum*-species recognized by OLIVER and previous authors, and the lumping of them to one species seriously hampers the discussion of their most interesting hybrids with other species. I therefore propose to raise them all to the rank of species. The name *D. longifolium* then must be kept for OLIVER's f. 2, as FORSTER's *Epacris longifolia* (and ROB. BROWN's *Dracophyllum longifolium*) clearly belongs to this species (type-locality Dusky Sound). Certainly this is a very compound species even in this restricted sense. — OLIVER's f. 3 is a rather different population, by COCKAYNE (1928 p. 205) apparently referred not to *D. longifolium* but to *D. Urvilleanum (sens. ampl.).* It consists of much smaller shrubs with much shorter leaves closely resembling those of *D. rosmarinifolium* (= *D. uniflorum* Hook. f.) and with smaller racemes somewhat approaching those of the *D. Urvilleanum* - group. When Mr. OLIVER and I stayed together at Manapouri, he kindly supplied me with good material of it from the bog E. of Manapouri mentioned by COCKAYNE. My own collections contain specimens of it from a bog in the lower Routebourn Valley (comp. below p. 375); probably also some somewhat deviating specimens with longer leaves from Maungatua should be referred to this species. When Mr. OLIVER and I discussed it in Wellington before my departure from New Zealand, he was also inclined to raise it to the rank of a species. I propose to attach his name to it as an appropriate acknowledgement of his excellent and much-needed revision of the genus. — As to OLIVER's f. 1, which includes the »*D. longifolium*»-population of the Auckland and Campbell Islands, HOOKER already pointed out the difference between it and the *D. longifolium* - population of New Zealand proper, and in his »Flora novaezelandiae» (1853) he even described them as two separate species. However, he referred o n e specimen from New Zealand proper, collected by FORSTER in Dusky Sound, to the subantarctic species, and therefore applied FORSTER's species-name *longifolium* to that species, while he gave the name *D. Lyallii* to the common species of New Zealand proper. Later on (1867) he again united the two species. Considering the geographical isolation of the two populations concerned, even the smallest c o n s t a n t difference between them should be sufficient to assure them the rank of separate species (comp. above p. 364). And as far as I know

Fiord Districts of South Island, the former species probably also extending further north. *D. prostratum* is a prostrate dwarf-shrub creeping and rooting in the peat of the extreme bog-communities (*Donatia-Oreobolus*-bog, *Sphagnum*-bog etc.[1]), while *D. Oliveri* is a low erect shrub hardly entering those communities. As far as I know, the two species mostly keep quite pure (the hybrid is not mentioned by OLIVER 1928), but in a *Sphagnum*-bog in the montane belt of the lower Routeburn Valley (W. of Lake Wakatipu, near the junction of the Routeburn and the Dart Valley), I found a most bewildering multitude of forms gradually connecting the two species and evidently belonging to the hybrid, which here showed a great vitality and quite outnumbered the pure species. This bog was of a very peculiar type, apparently offering both species suitable conditions in the same plant-communities.

I cannot refrain from mentioning a third example from the same genus in this connection, namely the *Dracophyllum*-population of Campbell Island, which I had some opportunities to study in collaboration with Mr. W. R. B. OLIVER. It consists of the two species *D. scoparium* (= *D. subantarcticum* Ckn) and *D. Cockaynianum* (= *D. longifolium* f. 1 in OLIVER's revision, comp. the note to

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there are even g r e a t constant differences between them: to those mentioned by OLIVER there must be added one very important difference, namely the constantly pubescent upper surface of the adult leaves (but not of the juvenile ones, a remarkable difference noted already by HOOKER 1847 p. 46) in the subantarctic population. In the true *D. longifolium* of New Zealand proper I have never seen anything like this pubescence; only in specimens from Stewart Island (Port Pegasus) I found a v e r y s l i g h t pubescence on the upper surface of the leaves (of much shorter hairs than in the subantarctic population). I therefore do not hesitate in proposing to raise also the »*Dracophyllum longifolium*» of the Auckland and Campbell Islands to the rank of a separate species. Could any name be more appropriate for this beautiful tree than *Dracophyllum Cockaynianum,* recalling the everlasting picture of subantarctic vegetation given by the grand old man of New Zealand Botany?

[1] In the subalpine belt, *D. prostratum* may be found also on dryer ground. It may then assume the life-form of a cushion-plant (on Bold Peak at the W. end of Lake Wakatipu I saw a big cushion sending out prostrate stems of the normal type). I have not been able to find any constant difference between this form and *D. muscoides* Hook. f. Specimens of the latter from the Old Man Range in Central Otago, kindly supplied by Mssrs G. SIMPSON and J. S. THOMSON, have just the same leaf-size as *D. prostratum,* not smaller as should be the case according to OLIVER 1928. If further field-studies should confirm the suspicion that *D. prostratum* and *D. muscoides* are only forms of one species, this species must be called *D. muscoides* Hook. f.

p. 374), and the hybrid between them (Cockayne 1928 p. 335, *D. insulare* Oliver l. c.). According to my own notes *D. Cockaynianum* was the dominant species (but mixed with *D. scoparium* and the hybrid in many forms) in much of the comparatively tall scrub traversed by myself on the southern side of Northeast Harbour, while in the literature the other species is always mentioned as the main dominant. Probably *D. Cockaynianum* may dominate only in the most protected tallest scrub, while the more low-growing *D. scoparium* plays the chief rôle in most of the scrub of the island; the latter species also grows dotted about in the open tussock-country (comp. Kirk 1891 p. 223, Cockayne 1904 pp. 274, 277). The hybrid appears to be abundant, fertile, vital, and very polymorphic, connecting the two species by a multitude of transitional forms. Nevertheless the two species have given all visitors the impression of two good and distinct units. This may be due to the comparative isolation of a large *D. scoparium* - population in the more open parts of the island. However, it may be well worth to look more closely into the *D. Cockaynianum* - population of the island, as I have some suspicions that all of it may be at least slightly »infected» with *D. scoparium* (the specimens I brought home from Campbell Island as pure »*D. longifolium*» have clearly shorter and more pubescent leaves than those from the Auckland Islands, where *D. scoparium* is lacking).

In this connection probably also the classical New Zealand hybrid *Coprosma propinqua* × *robusta* (*C. Cunninghamii* Hook. f.) should be mentioned (comp. Cockayne 1923, 1928, 1929, Allan 1924, 1926 *a, b,* 1929 *a*). Though both *C. propinqua* and *C. robusta* are distributed over at least most of the lowlands of New Zealand, they mostly appear to grow in different plant-communities (I got the impression that *C. robusta* is more at home in dense forest, while *C. propinqua* is frequently found also in more open scrubland). Especially in more or less swampy and not too dense forest they often meet (*e. g.* in Riccarton Bush at Christchurch, where this interesting hybrid-case was demonstrated to me by Dr. Cockayne and Dr. Allan), and then are connected by a very fertile and vital hybrid-population forming a complete series of transitional forms.

The examples given above all referred to species forming hybrids with full fertility and vitality but kept distinct by the adaptation of the two species to different habitats in the same main

distribution-area. The existence of large tracts of habitats suitable to one of the species but not to the other (and vice versa) guarantees, of course, the existence of pure populations of each species large enough to prevent the swamping of the two species to one large undifferentiated hybrid-population (comp. HAGEDOORN 1921). Just the same thing will happen when two species, forming a fertile and vital hybrid, have geographically different distribution-areas overlapping only to a comparatively small degree.

It is quite easy to find any number of good examples of such species-pairs. One of the best European examples is certainly the species-pair *Veronica longifolia* and *V. spicata*. *V. longifolia* is a comparatively hygrophilous species charactcristic for the alluvial meadows of North-eastern Europe, while *V. spicata* is a xerophilous stepp-species of more south-eastern distribution (STERNER 1922). In Sweden *V. spicata* has a typical southern distribution, while *V. longifolia* has its main distribution-area in the Northeast (comp. STERNER l. c.). A comparatively distinct subspecies of the latter species (subsp. *maritima*) is very common on the small exposed islands of the Swedish east-coast N. of lat. 58°. In the southern part of this distribution-area, *V. longifolia* subsp. *maritima* meets *V. spicata* and is connected with it by a fertile, vital and very polymorhic hybrid-population. In the province of Upland, only pure *V. longifolia* subsp. *maritima* is found in the outer belt of the archipelago, and (some clearly synanthropous colonies of *V. longifolia* excepted) only pure (or at least nearly pure) *V. spicata* in the inner part of the mainland. But between those belts there is a transitional coastal belt where the hybrid is common and mostly quite outnumbering the pure species (comp. ALMQUIST 1929 pp. 589—590). In a very rich collection made by me in the summer of 1908 in one of the classical localities for this hybrid (Fjäderholmarna in the harbour of Stockholm) there is a most bewildering multitude of hybrid-forms but not a single specimen that may be referred to either of the pure species. Probably both parent-species have entirely disappeared from this locality, the hybrid here appearing as a »Ganzwaise» in the sense of GAMS (1923). Still this hybrid-zone is of such a small extension compared with the vast areas in which only one of the pure species are found, that probably no botanist would get the idea to call *V. longifolia* and *V. spicata* »bad» species.

Another good example is the species-pair *Helianthemum nummu-*

larium and *H. ovatum* in South Sweden (comp. Du Rietz 1923 *b*, 1925). *H. nummularium* has a more eastern, *H. ovatum* a more south-western distribution in South Sweden. In the province of Blekinge, only pure *H. nummularium* is found in the east and only pure *H. ovatum* in the west, but in the middle there is a zone with both species growing together and connected by a fertile, vital and very polymorphic hybrid-population. In this hybrid-zone certainly no distinct limit can be traced between those species so distinct in the greater part of their distribution-areas.

A multitude of analogous cases have been described during the last decade from New Zealand in a series of important papers by Cockayne and Allan (1923—1929).

In several of those cases one of the two related species has a more northern and the other a more southern distribution overlapping only to a comparatively small extent. Those species may be quite distinct and very different-looking units in the areas where only one of them is present, and still join into one vast and most polymorphic hybrid-syngameon in the area where they are meeting. One of the best known examples for this type is the species-pair *Myrtus bullata* and *M. obcordata* (Cockayne 1918, 1923, 1929, Cockayne and Allan 1927, Cockayne and Phillips Turner 1928, Allan 1929). From the south of South Island up to about lat. 41° only pure *M. obcordata* is found, and in the northern part of North Island (north of lat. 36°) only *M. bullata* (except in two very small areas), but between lat. 41° and 36° both species frequently grow together connected by a most luxuriant transitional population of the very polymorphic hybrid (previously known as a species under the name of *M. Ralphii* Hook. f., demonstrated to me by Dr. Allan in Kitchener Park at Feilding).

In other cases one of the two species is restricted to the coastal scrub while the other has a wide inland distribution. *Hebe elliptica* and *H. salicifolia* form the best example for this type, the former one of the chief dominants of the coastal scrub of South Island (extending its distribution-area to the subantarctic islands of New Zealand and even to the Falkland Islands and subantarctic South America), the latter common in the lowlands throughout New Zealand and frequently meeting *H. elliptica* in the coastal scrub of South Island. In those places a highly polymorphic hybrid connects the two species (Cockayne 1923, 1925, 1928 p. 105,

Cockayne and Allan 1926, 1927, Allan, Simpson and Thomson 1926). Upon various forms of this hybrid the old species *Veronica (Hebe) amabilis* Cheesem. and *V. blanda* (Cheesem.) Pennell were founded. The high polymorphy and vitality of the hybrid is clearly demonstrated by the thorough analysis of Allan, Simpson and Thomson (l. c.). I saw it only in two localities (Punakaiki in the Northwestern District, where it was introduced to me by Dr. Cockayne and Dr. Allan, and Deep Cove in Doubtful Sound), but I got the impression that it does not enter the most exposed scrub, this being formed by pure *Hebe elliptica*.

In the New Zealand flora there are also several cases of one lowland and one mountain species connected by a luxuriant and highly polymorphic hybrid-population confined to a certain altitudinal belt. *Aristotelia serrata* is a large-leaved low tree common throughout the forested part of New Zealand up to about the lower limit for the prealpine forest-belt[1], *A. fruticosa* a small-leaved divaricating scrub having its main distribution-area in the prealpine and lower subalpine belts and in the dry low tussock region of the Eastern side of South Island, but also frequently occurring in the montane forest-belts (comp. Cockayne 1928, 1929). In these montane forest-belts the two species may not only be connected but even outnumbered by their very polymorphic hybrid (comp. Cockayne 1923, 1925, 1928, 1929, Cockayne and Phillips Turner 1928, Allan 1927 *a*, previously known as a species under the name *A. Colensoi* Hook. f.) which may ascend even a good bit higher than the pure *A. serrata*[2] (according to observations made in the Routebourn Valley together with Mssrs G. Simpson

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[1] I am using the term »prealpine belt» for the uppermost forest-belt of the New Zealand mountains (characterized by *Nothofagus cliffortioides, N. Menziesii, Libocedrus Bidwillii, Podocarpus Hallii* and *Dacrydium biforme* as main dominants in the tree-layer, by the constant absense of *Weinmannia racemosa, Metrosideros lucida* and other trees common in the montane forest-belts, and by a shrub-layer mostly very dense and more or less resembling the subalpine scrub, with which it has many species in common), restricting the term »subalpine belt» to the scrub and tall tussock belt above timber-line. Cockayne's (1928) »subalpine belt» thus includes both my »prealpine» and »subalpine» belts as well as parts of my »upper montane» belt. My terminology in this matter is based upon an attempt to work out a generally applicable terminology for the altitudinal vegetation-belts of the earth, that will be published shortly.

[2] Hybrids occurring in this way outside the range of o n e parent-species are called »Halbwaisen» by Murr (1919) and Gams (1923).

and J. S. Thomson). On the Ruahine and Tararua mountains, where this hybrid was first demonstrated to me by Dr. Allan, it appeared to be one of the most frequent shrubs of the montane and lower prealpine belts, and certainly posessed a vitality at least equalling that of the two pure species. — A similar case is that of *Coprosma grandifolia* and *C. tenuifolia*. The former is a large-leaved forest-shrub common in the lower forest-belts of North Island and northernmost South Island (= the *Beilschmiedia taraire*- and *B. tawa* - belts). The latter is a more small-leaved shrub confined to the higher forest-belts of the middle part of North Island (according to Cheeseman 1925 from Mt. Te Aroha and Hikurangi in the North to Mt Egmont and the Ruahine Mts in the South, and not recorded below 1000 ft). In this area also the hybrid is found (Allan 1928, Cockayne and Phillips Turner 1928, Cockayne 1929). After having made its first aquaintance on the Ruahine Mts with Dr. Allan, I got good opportunities to study it more closely during a stay in the Tongariro National Park (between Raurimu and Waimarino, on Hauhungatahi and at Ohakune). The hybrid is very polymorphic, forming a fine transition-series between the two species. As to its vitality, I got the impression that it was about as equally common and vital as both species. According to my notes, both species were common together with the hybrid up to the lower prealpine belt (= a little above 1100 m), where they disappeared simultaneously. However, what I brought home from the montane belt as pure *C. grandifolia* proved to be considerably more small-leaved than the guaranteed pure *C. grandifolia* of the lowland. I therefore have some doubts whether absolutely pure *C. grandifolia* really occurs on the Volcanic Plateau much above the upper limit of the tawa-belt (about 600 m). On the Tararua Mts, where *C. tenuifolia* is absent, I noted the highest isolated individuals of *C. grandifolia* at about 730 m, and in South Island it apparently does not much exceed the limits of the tawa-belt. So it may well look possible that the existence of a montane *Coprosma grandifolia* - population on the Volcanic Plateau may be due to the crossing of the pure *C. grandifolia* of the lowland with the more cold-resistant *C. tenuifolia*. As to the latter species, I hardly ever saw it isolated from the hybrid-population. It does not seem impossible that the whole *C. tenuifolia* - population has got the opportunity of being »infected» with *C. grandifolia*. So we m a y here have one of those troublesome

cases where hybridization has gone far enough to become a serious menace to the autonomy of at least one of the species involved.

This leads us over to the extreme cases in which the species are more or less lost in an overwhelming majority of highly polymorphic hybrid-populations. Many such cases have been described during the last decades by the Swedish school of salicologists (S. J. ENANDER, B. FLODERUS etc., comp. especially FLODERUS 1909, 1912, 1923, 1926 *a, b*) — and their views certainly cannot be lightly dismissed, as they are founded upon intensive field-studies carried out during half a century and extended over large parts of the Northern Hemisphere. In the later works of FLODERUS there is an increasing tendency to class most of the *Salix*-population of the arctic and subarctic regions as hybrids, and to restrict the species-concept to include only populations of the most extreme purity. Thus there are quite a lot of Swedish *Salix*-species that according to FLODERUS are hardly ever found pure in Scandinavia. As long as pure populations of those species are admitted to occur in other parts of their distribution-area, this method of treatment may be easily defended. But, if I have not misunderstood FLODERUS' recent papers, many of his species never form pure populations of any extension, those species thus being known o n l y as single individuals or very small populations accidentally found here and there in the highly polymorphic syngameons classed by FLODERUS as hybrids. In those cases it may well be asked whether we are not on a dangerous road that may easily lead to complete dissolution of any practically applicable species-concept in those populations.

If, as often happens, two *Salix*-species frequently hybridize in a certain region, and the hybrid is fertile, vital and easily crossed back with the two species, the genetical constitution of the two species-populations is easily changed to such an extent, that practically every individual of one of the species will show at least some slight traces of the other species. Thus, according to FLODERUS, the whole *S. nigricans* - population of the Scandinavian mountain-districts shows distinct traces of *S. glauca* and *S. phylicifolia, i. e.*, nearly every individual of *S. nigricans* in those districts has taken up at least some genes from the neighbouring *S. glauca*-and *S. phylicifolia* - populations. And according to the same author

the *S. nigricans* - population of South Sweden is constantly »infected» in the same way by *S. cinerea* (and often also with some other species). As a consequence of those statements FLODERUS refers practically the whole *S. nigricans* - population of North Sweden to the hybrids *S. nigricans* × *phylicifolia*, *S. glauca* × *nigricans* and *S. glauca* × *nigricans* × *phylicifolia* (or to hybrids of still more complicated constitution), while the *S. nigricans* - population of South and Middle Sweden is referred to the hybrid *S. cinerea* × *nigricans* or to other, more complex, hybrids. — In the same way FLODERUS treats the very polymorphic *Salix*-population of Greenland considered by him to be formed by the hybridizing of *S. arctica*, *S. chloroclados* and *S. glauca*. Most of the population of North Greenland is classed as *S. arctica* × *glauca*, most of that of Middle Greenland as *S. arctica* × *chloroclados* × *glauca*, and most of that of South Greenland as *S. chloroclados* × *glauca*. The pure species are considered to be rare, *S. glauca* being found over the whole country, but *S. arctica* lacking in the south and *S. chloroclados* in the extreme north.

This method of treatment, of course, involves the theory that the species distinguished are the primary units and the main population classed as hybrids is younger than those. This, however, is not proved. It appears quite possible that the smaller and more uniform populations classed as species are s e c o n d a r y units differentiated from the highly polymorphic syngameon classed as a complex of hybrids, or even only extreme forms accidentally appearing, disappearing and reappearing within this syngameon. In such a highly polymorphic syngameon any form of sufficient vitality may simulate a primary species if isolated, and to some extent even if not isolated. In a case like that of *Veronica longifolia* and *V. spicata* (comp. above p. 377), where it is quite obvious that the two species have immigrated from different directions (comp. STERNER 1922), the secondary nature even of a most vital hybrid-population may be taken as proved. The same may be said even of other highly polymorphic hybrid-populations occupying a comparatively narrow zone between two species widely distributed in their pure state. But as soon as the highly polymorphic hybrid-population is of a size equalling or surpassing that of the pure species-populations, suspicion may arise that the »hybrid» is older than the »species», and that the latter are simply secondarily isolated segregates of the highly poly-

morphic »hybrid». And this suspicion will be still stronger when the »species» do not even form pure populations but only appear as single individuals here and there in the highly polymorphic »hybrid». Good examples of cases in which very little or nothing talks in favour of the primary nature of the supposed »species», are furnished by GUNNARSSON's monograph of the genus *Betula* in Scandinavia (1925, comp. LOTSY 1925 *b* and ARWIDSSON 1930) — an unfortunate attempt to apply the Floderian *Salix*-method to a rather hopeless, highly polymorphic syngameon in another genus.

Polymorphic syngameons more or less analogous to those found in *Salix* and *Betula* are found also in several New Zealand genera. The genus *Alseuosmia* (Caprifoliaceae, forest-shrubs of the northern part of North Island), for instance, appears to consist of one vast and immensely polymorphic syngameon (COCKAYNE 1923, 1925, 1928, 1929, ALLAN 1926 *c*, COCKAYNE and ALLAN 1927), only conventionally divided in a few species of which COCKAYNE writes as late as 1929 (p. 21): »Whether there are really the above species of *Alseuosmia*, I have no idea.» What I saw of it in the field made me seriously doubt that it will ever be possible to get a natural division of it into species and hybrids. — *Senecio Lyallii* and *S. scorzoneroides* are two species of subalpine meadow-herbs distributed throughout the mountains of South Island and Stewart Island, mostly occurring together and then always connected by a highly polymorphic hybrid (COCKAYNE 1923, 1925, 1928). If I may rely upon my own observations, this hybrid quite often outnumbers the pure species. In this case it appears equally probable that the »species» are segregates of the hybrid as that the hybrid was formed by the meeting of two species originally isolated. If we follow the modern New Zealand taxonomists in considering the two species as valid, we probably here get a case similar to those of northern Salices, namely a hybrid playing a greater rôle than the pure species. — In the genus *Celmisia* several analogous examples are found. While in some sections of that genus the species are rather distinct, and the hybrids either sterile (comp. above pp. 365—366) or fertile but not vital enough, or at least not abundant enough to spoil the species-limits (*Celmisia coriacea* × *Traversii*, and *C. spectabilis* × *Traversii*, comp. COCKAYNE 1915, 1923, 1925, 1928 [1]),

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[1] A series of forms of these hybrids, collected by myself on the southeastern spurs of Mt Captain (Northeastern District), showed no reduction of the pollen-production.

there are other sections giving the impression of rather hopeless, extremely polymorphic syngameons analogous to the worst northern *Salix-* and *Betula*-populations. Thus the series of forms treated in CHEESEMAN's Manual as *C. brevifolia* and *C. novaezelandiae* gave me the impression of forming one very polymorphic syngameon (splendidly developed on Mt Wakefield in the Mount Cook region), probably only in some peripheral parts differentiated into pure populations of short-leaved (*C. brevifolia*) or long-leaved (*C. novae-zelandiae*) forms. Very nearly related and possibly intergrading into this syngameon is the very large and exceedingly polymorphic syngameon probably formed by *C. incana* Hook. f., *C. discolor* Hook. f., *C. intermedia* Petrie, *C. Bonplandii* (Buch.) Ckn, *C. Du Rietzii* Ckn and Allan, and perhaps some other species too. It is distributed throughout the New Zealand mountains. Round its margins smaller parts of it appear to have become isolated either in outlying mountains or on coastal cliffs [*e. g.* the northernmost subspecies of *C. incana* in North Island (comp. COCKAYNE and ALLAN 1927 p. 269), *C. holosericea* in the Fiord District, *C. Lindsayii* on the south-eastern coast of South Island], some of them differentiated as quite distinct species, but in its more central parts the syngameon presents, at least to the botanist making a comparatively short visit like myself, the picture of a most intricate network of rather different forms hopelessly mixed with each other and apparently all crossing. If this extremely polymorphic syngameon has been formed by hybridization of a number of more uniform species, the latter appear to have got lost at least to the same degree as many of the arctic species of *Salix* — but if my very incomplete impression of this vast syngameon may be of any value, I would rather believe that the small more uniform local populations occasionally found are simply secondary segregates of the highly polymorphic syngameon. How this syngameon first was formed is another matter — of course it may have been formed by the crossing of species differing from all those local populations presently found. But about this matter we had better confess our complete ignorance.

The practical taxonomical treatment of those large and highly polymorphic »hybrid»-syngameons in which the species have got more or less lost — or never have been differentiated — is one of the most difficult matters confronting the taxonomist of the present day. The Floderian method of picking out some more or less

rare forms as species, and classing the bulk of the syngameon as more or less complex hybrids between them, is possibly the most logical consequence of the methods applied to less complex syngameons. But the danger of this method is also quite obvious. Even if we admit that the frequency of vital »extravagant» forms in wild hybrids has been exaggerated by HERIBERT-NILSSON and other geneticists, attempting to prove the impossibility of determining wild hybrids without experiments, there is always a chance that a certain form intermediate between two others m a y have arisen from a cross of two other forms than those expected. And certainly the reconstruction of all those »triple»- and »quadruple»-hybrids in salicological literature is a very dangerous business. With full certainty we shall probably never know whether those highly polymorphic syngameons are not the result of early crosses of quite other species than those now differentiated in the outskirts of the syngameons.

The opposite extreme would be to treat the highly polymorphic syngameons simply as what they are at present, without any hypothetical considerations as to the species from which they are supposed to have originated by crossing. This would imply the naming of the highly polymorphic syngameons simply as species and the dividing of them into subspecies, varieties and forms, just as other compound and heterofacial species are divided. The extremely polymorphic *Salix*-population of Greenland mentioned above would thus be treated simply as o n e species and be divided into one northern subspecies (= FLODERUS' *S. arctica × glauca* + the rare individuals of pure *S. arctica* and pure *S. glauca* found in this region), one middle subspecies (= FLODERUS' *S. arctica × chloroclados × glauca* + the rare individuals of these three Floderian species in this region), and one southern subspecies (= FLODERUS' *S. chloroclados × glauca* + rare individuals of *S. chloroclados* and *S. glauca*). But I strongly fear that the consequent application of this method would lead to the dividing of the boreal *Salix*-population into very few and extremely compound species, very difficult to handle and each consisting of so extremely different forms that they would be of little value as units for ecology and all the other branches of botany that taxonomy has to serve. And I must confess that even my taxonomical mind strongly revolts against the idea of lumping two so different populations as pure *Salix arctica* and pure *S. glauca* into one species.

Still I think this method is the only one applicable in the case of *Betula*, the Scandinavian *Betula*-population probably containing only two recognizable species, *Betula nana* and *Betula alba* (connected by a highly polymorphic hybrid of too moderate vitality to spoil the species-limit). Also in the cases of *Alseuosmia, Senecio Lyallii-scorzoneroides,* and the *Celmisia discolor* - group it may be sound to try this method parallelly with the others.

The third method possible is a compromise, used at present by many Scandinavian taxonomists and ecologists, whose limited knowledge in the mysteries of modern salicology has simply forced them to adopt it in their field-work. According to this compromise-method, the species are simply delimited in a less rigorous sense than the Floderian one, and only the forms clearly intermediate between the pure species are included in the hybrids. The establishing of triple- and quadruple-hybrids is generally avoided except in quite undisputable cases. This method implies the admission that a part of a species-population may be changed s l i g h t l y by »hybridogenous infection» of other species and still remain within the limits of the species concerned. Considering the great polymorphy admitted in many species when due to other causes, this appears to be a rather sound admission. Of course it will then be a purely practical question where the limit between the hybrid *sensu stricto* and this species *sensu amplo* should be drawn. By this method most of the *Salix nigricans*-population of South and Middle Sweden is simply classed as *S. nigricans,* in spite of its apparent hybridogenous infection of *S. cinerea* etc., and most of the North-Swedish *S. nigricans* too, in spite of the infection of *S. phylicifolia* and *S. glauca.* How the *Salix*-population of Greenland mentioned above should be treated according to this method I do not know, but possibly a good deal of it would come in under the species *S. arctica sens. ampl., S. glauca sens. ampl.,* and *S. chloroclados sens. ampl.* [= *S. groenlandica* (Anderss.) Lundstr.]

Syngameon, commiscuum and convivium.

In the above discussion l have consequently used LOTSY's term »syngameon» in a rather wide sense, *i. e.* as a short and handy term for any intercrossing population not divided by distinct lines or zones of discontinuity. A syngameon in this sense may be either a c o m m i s c u u m or a part of a commiscuum in the

sense of Danser (1929 *a, b*). According to Danser, a commiscuum includes a l l individuals connected by a genetical possibility of »Vermischung», *i. e.* exchange of genes. Populations prevented from crossing only by geographical isolation according to Danser still belong to the same commiscuum, but each of them forms a separate c o n v i v i u m (Danser 1929 *b*). According to the definition and the examples given by Danser, his convivia are identical with the »species» of Hagedoorn 1921, *i. e.*, any population more or less differentiated from its relatives and tending to reduce its potential polymorphy may be called a convivium. As the convivia of Danser must only be »mehr oder weniger scharf unterscheidbar», they may in some cases correspond to our species, in other cases to our subspecies or even varieties (this is clearly shown not only by Danser's definition but also by his examples). A commiscuum, on the other hand, is often identical with a species, but it may also include several species, if they are actually connected by fertile hybrids, or if they are prevented from being so only by geographical isolation.

An important fact pointed out by Danser is the possibility of »Vermischung» (exchange of genes) of two biotypes, even if they are not fertile with each other, but both form fertile crosses with a third biotype. Thus it is not necessary that all biotypes in the same commiscuum (or in the same syngameon) should be capable of d i r e c t crossing. The occasional occurrence of intraspecific sterility pointed out by several geneticists (comp. for instance Winge 1926 *a*, Turesson 1929 *a*, Münzing 1929, 1930) does not therefore affect the validity of our species-definition.

Practical methods of species-taxonomy.

From what has been said above regarding the delimitation of species it will be clearly seen that the pure »abstraction»-method of species-making by sorting specimens into groups merely after their morphological resemblance, as still practised by many taxonomists [and still supposed by Lotsy (1921, 1925 *b*) and many other geneticists to be the method of a l l taxonomy], must be firmly rejected, and that the »morphologic-geographical method» so brilliantly advocated and demonstrated in the 'nineties by Wettstein and his followers, must come to its right again not only in zoology, where it has been practised with eminent results during the last decades, but also in botany, where it unfortunately appears to

have fallen into some discredit or oblivion after the Wettsteinian period. It must not be forgotten that taxonomy not only deals with abstract concepts, but in the first line with living populations. And certainly those populations must be studied in the field much more than is mostly the case in present-day taxonomy. Though I am inclined to think that COCKAYNE and ALLAN are somewhat underrating the possibilities of studying a population by means of herbarium-material (if this material is well preserved and rich enough to give not only examples of the populations concerned but also some idea of the regional and local variability of its polymorphy), their strong emphasizing of the need of F i e l d-T a x o n o m y certainly cannot be supported enough (comp. also FRIES 1852 pp. 194—210, SAMUELSSON 1922 p. 229, HALL and CLEMENTS 1923 p. 15, DU RIETZ 1930 p. 295). And certainly there is something fundamentally wrong with taxonomy as long as many of those who are put to carry out most of the monographical work, namely the officials of the great botanical museums, are forced by antiquated regulations to spend practically all their time in indoor museum-work — while a modern botanical museum-official, of course, ought not only to be allowed but even forced to spend at least several months of the year in field-study of the populations he has to deal with in his museum during the rest of the year.

The importance of genetical methods in species-taxonomy cannot, of course, be overrated — as long as those methods are not supposed to r e p l a c e the study of wild populations in their natural habitat, or the necessary comparative museum-work with those populations. If we take home a single specimen (or a few specimens) of each species, of each subspecies, or even of each variety of a genus, plant them in our gardens, cross them with each other and play with them in various ways, they will still tell us nothing about the variability of polymorphy in the wild populations concerned, *i. e.* nothing of what is most essential for grasping the species and their subordinate units. The field-study of the variability of polymorphy in wild populations can be replaced as little by the study of a few living individuals brought home to a garden as by a few dry individuals in a museum, and it is often of more use to get a number of dry individuals sufficient for getting at least some idea of the variability of polymorphy in the wild population than it is to get an i n s u f f i c i e n t number of living individuals to a garden. The claim of TURESSON (1926 *c*)

and other geneticists to have replaced the old »descriptive taxonomy» with a new »experimental taxonomy» must therefore be firmly disputed. In this statement there lies no underrating of the importance of garden-experiments as a c o m p l e m e n t to the comparative field-study combined with comparative museum-work. But even the elimination of the phenotypical variability of a population can certainly be done to a much greater extent by means of a comparative field-study, than is admitted by most geneticists believing this to be possible only in their experimental gardens.

The practical methods of d e s c r i b i n g s p e c i e s cannot be discussed here in any detail. Still it must be mentioned that the general recognition of species as populations, mostly consisting of a great number of forms often grouped to distinct local and even regional facies (varieties and subspecies), makes a revision of the traditional method of describing species rather necessary. At present a diagnosis of a species may be founded upon one individual or upon several individuals belonging to one or several forms, varieties or even subspecies — and about this mostly nothing at all is told in the diagnosis. When the diagnosis tells us that the leaves have a certain variability, nobody knows whether this refers to one individual or to many individuals, nor what the relation is of those many individuals to each other. The recent proposition of GALLÖE (1928) that a diagnosis of a species should be founded upon one single individual, must certainly be taken into serious consideration — but of course this description of one single individual cannot be sufficient to characterize the species concerned. The best method would probably be to give 1) one diagnosis of the type-individual, 2) one description of the polymorphy of the type-variety (*i. e.* the local population to which the type-individual belongs), and 3) one description of the variability of polymorphy in the whole species. If distinct subspecies are differentiated, also the variability of polymorphy in those should, of course, be separately described. If many branches are taken from a shrub or a tree and placed upon different herbarium-sheets, all of these must, of course, be considered parts of the type (not co-types, as often practised at present). If, on the other hand, several individuals of small plants are placed upon one herbarium-sheet, only o n e of them may be designated as the type (not the whole sheet, as is the present practice). The

term »co-type» ought then to be restricted to individuals taken in the same locality as the type and supposed to belong to the same biotype or being at least practically indistinguishable from the type (very often the type forms a part of a clone or a more or less autogamous and inbred population of practically undistinguishable individuals).

The practical application of this method I hope to be able to demonstrate shortly in another paper.

11. **The hybrid.**

A hybrid is a population intermediate between two or several different species, supposed to be originally formed by the crossing of biotypes belonging to different species.

This hybrid-concept probably coincides with what most biologists have called and still call a hybrid. As mentioned above (p. 342), however, also another very different hybrid-concept has been advanced during the last decades. According to LOTSY (1916 etc.) and RAUNKIAER (1918) every heterozygous biotype should be called a hybrid. As the strict consequence of LOTSY's and RAUNKIAER's hybrid-definition turns out to be that every sexual species in our sense would consist exclusively of hybrids *sensu* LOTSY (even according to LOTSY's own opinion, comp. above p. 341), the practical applicability of this hybrid-concept appears at least rather dubious. Practically, even LOTSY himself does not use it strictly in his own hybrid-studies, using the term »hybrid» only for biotypes intermediate between two »Linneons» (= our species, comp. for instance LOTSY and GODDIJN 1928). Still this is something rather different from our hybrids. For highly polymorphic hybrids in our sense LOTSY (l. c.) uses the terms »hybridogenous populations» (»populus hybridogenus»), »hybridogenous crowd», »hybrid swarm» etc. LOTSY's hybrid-terminology is adopted also by COCKAYNE and ALLAN (1923—1929), who use the term »hybrid» for any biotype intermediate either between two species or between two »jordanons» (comp. above p. 350), and the term »hybrid swarm» for any highly polymorphic hybrid in our sense.

The various types of hybrids in our sense have been dealt with in detail above in connection with the species; so no further dis-

cussion of them is necessary. Like a sexual species, a hybrid may be more or less polymorphic, consisting of a very great number of biotypes. In fertile and highly polymorphic hybrids these biotypes form a syngameon just like the biotypes in a sexual species. Between a highly polymorphic hybrid and a highly polymorphic species there is no fundamental difference, and therefore it is often very difficult to decide if a highly polymorphic population should be classed as a species or as a hybrid. A highly polymorphic hybrid may develop to one or several species by more or less effective isolation from the parent species. Still most highly polymorphic hybrids are considerably more polymorphic than most species, and the high potential polymorphy of the hybrid is then protected from being reduced by the constant crossing back with the two parent species, and the constant appearing of new crosses between them. Using HAGEDOORN's (1921) species-definition we may say that a species tends to reduce its potential polymorphy, while a hybrid does not tend to reduce it — if not isolated from the parent species, in which case it either disappears or assumes the character of a new species.

The discoveries of cytological anomalies in many hybrids during the last decades have made some botanists believe that cytology is always able to tell whether a certain biotype belongs to a species or to a hybrid. Unfortunately this is not the case. There is no constant fundamental cytological difference between species and hybrids. Some hybrids (between species with different chromosome-number) are easily recognized by cytological anomalies (but then mostly also by reduced fertility or at least vitality), but other hybrids (between species with the same chromosome-number) are even cytologically indistinguishable from their parent species.

During the last years there has been much discussion regarding the methods of naming hybrids. The traditional method of using a formula consisting of the names of the parent species (e. g. *Veronica longifolia* × *spicata*, *Dracophyllum filifolium* × *recurvum*) is clear but not very handy. Many botanists therefore give a binary name also to hybrids (e. g., × *Veronica hybrida*, × *Dracophyllum arcuatum*) which is used alternating with that somewhat complicated hybrid-formula. This may be convenient when it is uncertain whether the population concerned should be classed as a species or as a hybrid, but in other cases it appears to imply the burdening of nomenclature with a rather unnecessary name.

In the International Rules, the giving of binary names to hybrids is recommended »whenever it seems useful or necessary» (Art. 31). The method of naming hybrids by abbreviated formulae as proposed by COCKAYNE and ALLAN (1926 *c*, 1927 etc.), is certainly very handy in verbal discussions, notebooks etc., but for botanists less familiar with the flora concerned it may often be hard to understand that *Nothofagus cliffusca* means *Nothofagus cliffortioides* × *fusca*, *Hebe ellipsala Hebe elliptica* × *salicifolia*, *Aristotelia fruserrata Aristotelia fruticosa* × *serrata*, *Ranunculus Buchlyallii Ranunculus Buchananii* × *Lyallii*, etc. In scientific literature I therefore prefer writing out the whole formula. COCKAYNE and ALLAN severely criticize the method of giving binary names of the ordinary type to hybrids, pointing out that most of those binary names in use were originally given only to o n e form or a small group of forms within a highly polymorphic hybrid-population, and therefore cannot be considered representative for the whole hybrid. This is certainly quite right, but just the same may be said of most species-names also, though the matter perhaps becomes more disturbing in polymorphic hybrids because of the great differences between the form originally described and many other forms of the hybrid. To me it appears to be merely a matter of taste and convenience, whether we use those old species-names or the abbreviated formulae of COCKAYNE and ALLAN as more handy substitutes for the complete hybrid-formulae.

12. The units superior to the species.

The taxonomical units superior to the species can hardly be called »fundamental» to the same degree as the species and its subordinate units, since the delimitation of the higher units is to much greater an extent a matter of taste and convenience. Every taxonomist knows how hopelessly opinions differ regarding the delimitation of genera and other units of higher rank. It is not my purpose to discuss those higher units in any detail in this paper. Only some of the general principles for the delimiting of those units will be briefly discussed here.

As was shown above (pp. 352—353), it is quite easy to understand the differentiation of a species into regional and local facies in the light of what I would propose to call HAGEDOORN's l a w o f

differentiation by means of automatic reduction of potential polymorphy — even without the assumption of any rôle played by induced or non-induced mutations, nor by selection. In this connection it was also mentioned that just the same process may often lead to the differentiation of a syngameon into different species, if the syngameon is split up into parts more effectively isolated from each other. This effect of isolation was clearly recognized already by LEOPOLD VON BUCH (1825, comp. WAGNER 1889 p. 344) and MORIZ WAGNER (1868—1889), and this idea was built out to an elaborate theory by the latter author (the »migration-theory», later changed to the »separation theory»). But the mechanism of differentiation in the absence of any mutation could, of course, not be recognized by those authors (though the importance of inbreeding was clearly pointed out by WAGNER, comp. for instance 1889 p. 401), as this recognition depends upon genetical experiences not available at that period (comp. HAGEDOORN 1921 p. 120). Of course nobody knows what would have happened, if MENDEL's work (1865) had been known to WAGNER, and HAGEDOORN (1921 p. 120) may be right in assuming that »WAGNER would have greatly appreciated it, and could have been trusted to incorporate it into a really logical evolution-theory». As it was now, however, WAGNER had to look for another explanation to the effect of isolation, and he believed to find that explanation in the production of new forms (mutations), to a great extent directly induced by the environment (as assumed also by VON BUCH) and saved by isolation from being swamped in the original main population [the clearest summary of his views in this respect is probably found in pp. 472—473 in his »Gesammelte Aufsätze» (1889)]. He strongly opposed DARWIN's selection-theory (1859), considering the struggle for life to be »nur eine unwesentliche begleitende Erscheinung der Differenzierung, d. h. ein nur zeitweilig mitwirkender und nebensächlicher Faktor dieses Prozesses» (WAGNER 1889 p. 462[1]). Unfortunately WAGNER's ideas found

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[1] Many years after WAGNER's death, his opposition in this point was characterized by HAGEDOORN (1921 p. 120) in the following words:

»DARWIN lacked the necessary key at the time when he needed it most, and when he came into touch with WAGNER's work, it could not shake his faith in selection as the cause of stability of species. All the recent work in Genetics, MENDEL's law, the things we have since learned about the nature of the genes, the selection experiments with the most diverse material, have shown us that WAGNER in opposing DARWIN in this fundamental point had the right wholly on his side.»

little recognition both in the dominating Darwinian school of his time (comp. for instance DARWIN 1869 pp. 119—122, HAECKEL 1868, WEISMANN 1868, 1872, SEIDLITZ 1871, and WALLACE 1889) and among anti-selectionists like NÄGELI (1872, 1884). But the idea of isolation as the dominating factor in the formation of new species got new strength by the fundamental works of GULICK (1872—1905) and ROMANES (1886, 1897). While WAGNER had recognized the import-ance of s p a t i a l isolation only, GULICK and ROMANES — independ-ently of each other — were the first to realize the full import-ance of p h y s i o l o g i c a l isolation, and to work out »the general theory of isolation» summarized by ROMANES (1897 p. 145) in the following words: »Without isolation or the prevention of free intercrossing, organic evolution is in no case possible.» In the first years of the new century, similar lines of thought were followed by MAYER (1902), D. S. JORDAN (1905), K. JORDAN (1905) and several other authors, and in the last decades the idea of isolation as the main factor in species-formation has steadily won new ground among biologists[1].

Parallelly with this development the traditional theory of a divergent evolution has gradually lost ground, not only among geneticists but also (earlier than among geneticists and certainly unnoticed by most of them) among those ecologists carrying out field-studies of plant and animal distribution. In 1906, GUPPY advanced his d i f f e r e n t i a t o n t h e o r y, founded upon extensive studies of plant-distribution and worked out more elaborately in a series of subsequent publications (comp. for instance GUPPY 1907 and 1917), and in 1907 very similar views were expressed by WILLIS (comp. also WILLIS 1922, 1923), independently of GUPPY but founded upon analogous researches in other parts of the world. According to GUPPY's differentiation theory, »the rôle of the polymorphous species belongs alike to the plant and to the bird. A species that covers the range of a genus varies at first in every region and ultimately gives birth to a new species in some parts of its range. Then the wide-ranging species disappears and the original area is divided up into a number of smaller areas each with its own group of species. Each smaller area breaks up again, and forms, yet more specialized, are produced; and thus the process of subdivision of range and of differentiation of form goes

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[1] Of more recent authors clearly opposing this idea, H. DE VRIES (1903 p. 507) must be specially mentioned.

along until each island in an archipelago owns its bird and each hill and valley has its separate plants.» (GUPPY 1906 p. 522.) The contrast between this theory and the traditional theory of divergent evolution is summarized by WILLIS (1922 p. 221) in the following very suggestive way: »Chiefly important among these is the new view of evolution, first proposed by GUPPY in 1906, and by the writer in the following year, that evolution did not proceed from individual to variety, from variety to species, from species to genus, and from genus to family, but inversely, the great families and genera appearing at a very early period, and subsequently breaking up into other genera and species.»

As to the mechanism of this differentiation-process, GUPPY and WILLIS accepted mutations arising independently of the environment as the evident cause, and rejected both selection and »direct adaptation» as factors of any importance. Similar views are found in the works of CRAMPTON (1917, 1925 *a, b*). As to isolation, none of these authors appears to have fully recognized its fundamental rôle in the differentiation-process. And probably there is not much need of isolation for the explaining of this differentiation-process, if we count with mutation to such an extent as these authors did — especially if with l a r g e mutations like those assumed by WILLIS — just as DARWIN's strong belief in the great power of selection made him regard isolation as a factor of minor importance.[1]

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[1] As has recently been pointed out by EKMAN (1928, 1929), many recent geneticists have made a great mistake in accusing DARWIN of having believed selection to be able to p r o d u c e new biotypes. The production of new biotypes forming the material for selection DARWIN explained by non-induced mutation (»variation»), and to some extent (especially in his later works) by mutation induced by the environment. But certainly he believed in the power of selection to change a population by favouring even mutations differing in the most minute and insignificant characters from the main stock of the population — and in this belief he was followed by WALLACE, WEISMANN and other selectionists of the Darwinian period. Therefore he thought himself able to explain the remarkable differentiation of species in the Galapagos Islands by the minute differences in the c o m p e t i t i o n f a c t o r s of the different islands, which he thought sufficient to lead to the favouring of different mutations in the different islands (even if the same mutations were produced in them all). However, he confessed that the lack of differences in the h a b i t a t of the different islands for a long time appeared to him as a great difficulty (DARWIN 1859 p. 400). What a small rôle he alotted to the pure isolation-factor is clearly seen both in his publications (comp. for instance 1859 p. 402, 1869 pp. 119—122) and

Quite independently of GUPPY and WILLIS, the differentiation-theory was advanced again in 1916 by CAJANDER (1916 pp. 561—562, comp. also 1921) and LOTSY (1916, comp. also 1912—1914). CAJANDER explained the differentiation-process partly (and apparently in first line) by selection, partly by mutation; he also pointed out that it resulted not only in geographical races and geographically vicarious species, but also in e c o l o g i c a l races and ecologically vicarious species (»Standortsrassen» and »Standortsarten»). LOTSY, on the other hand, did not accept any mutation-theory, but explained the differentiation-process simply by isolation (spatial or physiological) in connection with selection. Similar views were expressed by HERIBERT-NILSSON (1918). Already in 1917 J. SCHMIDT had pointed out that besides selection »pure accidents» must be an important factor in the differentiation of local races in *Zoarces viviparus* (comp. above p. 349) But it was first HAGEDOORN (1921) who showed the way to a real understanding of the differentiation of a syngameon by isolation even in the absence of any selection (and of any mutation), t h u s m a k i n g the d i f f e r e n t i a t i o n - t h e o r y q u i t e i n d e p e n d e n t o f all the c h a n g i n g t h e o r i e s r e g a r d i n g t h e e x i s t e n c e of e f f e c t i v e s e l e c t i o n a s w e l l a s o f i n d u c e d o r n o n - i n d u c e d m u t a t i o n.

During the last decade, the differentiation-theory has been accepted by several authors. TURESSON (1922—1929) followed the same main channels of thought as LOTSY, J. SCHMIDT and CAJANDER, studying the differentiation of species into »ecotypes» (partly corresponding to CAJANDER's »Standortsrassen», partly to his geographical races, comp. also above p. 355) and explaining this differentiation mainly by selection. The present author (DU RIETZ 1923 *a*) applied the same point of view upon the differentiation of species, pointed out the insufficiency of selection for its explanation, and, rejecting mutation as a probable factor of importance, emphasized

in his letters to WAGNER (comp. WAGNER 1889 p. 350, ROMANES 1897 pp. 103—106). Under those circumstances it is important to note that in earlier years DARWIN had expressed a much higher appreciation of the rôle of isolation; in 1844 he declared in a letter to HOOKER, that »with respect to original creation or production of new forms... isolation appears the chief element» (ROMANES 1897 pp. 101—102). Evidently this was the primary impression left by the field-studies of his youth, but under the influence of his later speculations and work with domestic animals and plants it gradually faded away and was replaced by the theory of natural selection.

the importance of purely accidental differences in the original composition of isolated parts of a syngameon. Among other recent contributors to the differentiation-theory, BERG (1926), DANSER (1929 *a, b*) and BAUR (1930 pp. 399—400) must be specially mentioned.

If we take the existence of this process of differentiation of a highly polymorphic syngameon into species as a fact — and I really think we have the right to do this now — we may leave the question of how those syngameons were originally formed provisionally open, and try to look into the possible bearing of this differentiation-process upon the practical delimitation of the taxonomical units superior to the species. In those cases where it is obvious and undisputable that a number of species have been differentiated out of one original syngameon, the desirability of uniting all those species to a unit of higher rank has been felt by several authors. If the differentiation is due only to geographical isolation, *i. e.* if a series of »vicarious species» (»echte Vikaristen» *sensu* VIERHAPPER 1919) with only o n e species in each of the isolated districts (islands, mountains etc.) is formed, those species form an »Artenkreis» in the sense of RENSCH (1929) and a »Formenkreis» in the sense of KLEINSCHMIDT (1901—1926), who does not recognize the difference between the two types of units separated by RENSCH as »Artenkreise» and »Rassenkreise». A good example of a natural group of species of this type is formed by the three vicarious species of *Gentiana* in the subantarctic islands of New Zealand mentioned above (p. 364).

If the differentiation is due not only to geographical but also to ecological or physiological isolation, there is often not o n e species in each district corresponding to one species in each of the other districts, but a group of several nearly related species in each district corresponding to an analogous group in each of the other districts. In such a case I have mostly found RENSCH's »Artenkreis»-concept unapplicable, as it is often impossible to say that one of those nearly related species in a certain district is more corresponding to a certain species in another district than the others. In the genus *Dracophyllum* in New Zealand, for instance (comp. OLIVER 1928), there are only a few examples of clearly vicarious species forming distinct »Artenkreise» *sensu* RENSCH (one of the best is that of the two tuft-tree species *D. recurvatum* in North Island and *D. Traversii* in South Island). But most of

the New Zealand species of *Dracophyllum* form a network of species combining certain characters in the most various ways, and occurring together in more or less overlapping distribution-areas in such a way that it is not possible to group them into distinct »Artenkreise», but only into dubious »Artenkreise» i n s e v e r a l a l t e r n a t i v e w a y s. If, for instance, life-form and habitat are taken as base for the grouping, the subalpine dwarf-shrub heath species *D. recurvum* (in the central part of North Island, comp. above p. 373) and *D. pronum* (South Island) may be grouped to one »Artenkreis», while *D. filifolium* (one of the dominants of the North Island subalpine scrub, comp. above p. 373) forms another »Artenkreis» together with *D. rosmarinifolium* (= *D. uniflorum* of the older literature, one of the dominants of the South Island subalpine scrub). But if we take the leaves or the flowers as base, *D. recurvum* and *D. pronum* must be placed in quite different »Artenkreise», and the same will be the case with *D. filifolium* and *D. rosmarinifolium.* According to the position of the flowers (a character considered to be of great taxonomical importance in *Dracophyllum*), *D. rosmarinifolium* could also be united with *D. subulatum* (on the Volcanic Plateau of North Island) and some other species into an »Artenkreis» not less natural than the one mentioned above.

The method of grouping geographically vicarious species into »Artenkreise» appears thus to be applicable only in special cases. Another method is the grouping of the species forming hybrids fertile enough to allow »Vermischung» (exchange of genes) in nature or in cultivation, into one c o m m i s c u u m in the sense of DANSER (comp. above p. 387), and of the commiscua forming more or less sterile hybrids into one c o m p a r i u m or »Bastardierungs-genossenschaft» (DANSER 1929, *a*, *b*). The whole section *Lapathum* of the genus *Rumex*, for instance, according to DANSER forms one comparium. And of the New Zealand species of *Nothofagus* four (*N. fusca, N. cliffortioides, N. Solandri* and *N. truncata*) probably form one commiscuum, while the fifth species (*N. Menziesii*) forms not only its own commiscuum but probably even its own comparium (comp. COCKAYNE 1926, COCKAYNE and ATKINSON 1926).

Probably it will be found possible to work out a synthesis of the method last mentioned with the geographical method mentioned above, enabling us to reconstruct many of the old syngameons from which the present species have been differentiated. As a

matter of fact, many of the sections, subgenera and genera distinguished in present-day taxonomy, especially those with a rather restricted distribution, give the impression of being old well-defined syngameons split up into a number of species in the way described above.

It cannot be discussed here in any detail what rôle selection and induced or non-induced mutation[1] may have played during this differentiation-process. In the discussion above, I have only talked of the process of differentiation by means of automatic reduction of polymorphy, b e c a u s e n o o t h e r p r o c e s s a p p e a r s to b e n e e d e d t o e x p l a i n w h a t we s e e i n n a t u r e, and because this is the only process about which we know anything with full certainty. But, as mentioned above (p. 353), this differentiation process may be supported by selection (or rather by heterogenous elimination), if the isolation takes place in obviously differing habitats. And it would be unscientific to deny the p o s s i b i l i t y that even induced or non-induced mutation may play a rôle in that process, though I must admit that I (like LOTSY, HERIBERT-NILSSON, HAGEDOORN, DANSER and other recent authors) am unable to find much talking in favour of this assumption. As to the rôle of selection, my field-experience in various parts of the world and in various groups of the vegetable kingdom has brought me to exactly the same conviction as that of WAGNER (1868—1889), GUPPY (1906—1917), WILLIS (1907—1923), HAGEDOORN (1921), HAYATA (1921 —1928), TOWER (1922), LOTSY (1925 a), PARR (1926), and many other authors, namely that the rôle of selection has been much overrated, and that it mainly consists of the elimination of biotypes absolutely unviable in a certain habitat (DU RIETZ 1929 p. 422). Nobody has expressed this better than LOTSY (1925 a p. 59): »We have no evidence that it is the fittest, the best adapted, which

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[1] The term »mutation» is used here to designate 1) any genotypical change, small or large, continuous or discontinuous, that is not due merely to recombination of genes, and 2) any new biotype produced by such a change. Especially in America that term is still sometimes used also in the sense of BURBANKS, i. e. as a designation for biotypes originating from a cross and exhibiting characters not present in any of the parents (comp. HAGEDOORN 1921 pp. 84—85, 154—155 etc.), or »extravagant» biotypes in the sense of HERIBERT-NILSSON (1918). Such appearing of new characters simply as the result of a recombination of genes (»Amphimutation» in the sense of PLATE 1913 p. 497, 1914 p. 138) is n o t included in the mutation-concept used here (which corresponds only to PLATE's »Neo- oder Idiomutation»).

survives in the struggle for life; all we can say is that it is the survivals which survive, and this is probably, just as in a railway accident, more determined by a happy position than by any particularity of structure.» A critical study of the correlation between life-form and habitat in various parts of the world has made me believe that this correlation is much overrated in botanical literature, and that only life-forms absolutely unviable in a certain habitat are eliminated in this habitat, while chance and historical factors, but not superior or inferior adaptation, mostly determine the main composition of the vegetation (Du RIETZ 1929 p. 422) — just as is the case in the human population! This certainly speaks neither in favour of the theory of positive selection nor of that of mutations partly induced by the habitat. But to all those problems I hope to come back in another publication.

As to the rôle of hybridization in the differentiation of syngameons into separate species, we unfortunately know very little. Evidently it must often happen, that the differentiation-process is counteracted by the occasional meeting and crossing of two species spatially — geographically or ecologically — isolated, but still belonging to the same commiscuum (*e. g. Veronica longifolia* and *V. spicata,* comp. above p. 377) — or *Abies alba* and *A. cephalonica,* which according to MATTFELD (1930) were geographically differentiated from a common stock during the Tertiary period but brought together again by the Glacial period, producing the highly polymorphic hybrid *A. Borisii regis* now connecting the *A. cephalonica*-population of Greece with the *A. alba*-population of the northern Balkan Peninsula). Equally clear is that this must often give rise to »extravagant» forms, and even that some of them — as well as some of the more intermediate forms — may happen to become isolated and then be vital enough to develope into new species.[1] It is quite clear, that the actual polymorphy

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[1] The theory of species-production by means of hybridization can be traced back as far as to LINNÆUS, who already in 1744 (Peloria) expressed the belief that new species, and even genera, could be formed by hybridization. In 1760 (De sexu plantarum) he advanced the theory that there had originally been only one species in each genus, all the other species being formed by the crossing of that species with species belonging to other genera. (A good summary of the genetical views of LINNÆUS, which were fundamentally different from those ascribed to him in most of the evolutionistic and genetical literature, is given by ALMQUIST 1917). — In 1820 W. HERBERT, on the base of extensive hybridization-experiments, expressed the view that the present species of each main

of a commiscuum may be heightened in this way, but not its potential polymorphy (comp. Danser 1929 *b*), and all the new forms produced in this way may very well have been rea-

group of plants had »been produced by variation of soil, temperature, or humidity», and »that such diversity might have been further multiplied by hybrid intermixture, as the species were brought together by the natural progress of their diffusion» (HERBERT 1820 p. 17). Later on, the hybridization-theory has been repeatedly advanced by many authors. Already in 1863 CH. NAUDIN, who had expressed similar views himself as early as 1852 (comp. FOCKE 1881 pp. 505 and 509), wrote that »plusieurs botanistes d'une grande autorité croient que certains hybrides fertiles, sinons tous, peuvent se fixer et passer à l'état de variétés constantes, c'est-à-dire de véritables espèces» (NAUDIN 1863 p. 196); among those botanists E. REGEL specially mentioned. In 1871, A. KERNER published his first essay on the formation of species by hybridization, and in 1881, he and L. REICHENBACH were mentioned as the chief advocates of this theory by FOCKE (1881 p. 506), who also believed, that »ein grosser Theil der neuen Arten zwar nicht plötzlich, aber doch mittelbar aus Raçenkreuzungen hervorgeht» (p. 509). In 1891 (and 1898), KERNER gave a more complete account of his »Vermischungstheorie» stating that »alle in der Nachkommenschaft sich erhaltenden Veränderungen der Gestalt durch Kreuzung, beziehentlich durch Vermischung zweier ihrer Konstitution nach verschiedener Protoplasten zu stande kommen» (KERNER 1898 p. 536). — In recent literature WEISMANN is often mentioned as one of the originators of this theory — WIESNER (1902 p. 259) even talks of »die WEISMANN-KERNER'sche Vermischungstheorie». This appears to be in bad accordance with the following passage in WEISMANN'S last work (1913 II p. 304): »Einzelne Botaniker, wie KERNER V. MARILAUN, sehen in der Vermischung der Arten ein Mittel zur Bildung neuer Arten mit besseren Anpassungen; sie lassen fruchtbare Bastarde unter Umständen die Stammarten verdrängen und selbst zur Art werden. Man wird zugeben können, dass solche Fälle vorkommen ... aber man wird dennoch behaupten müssen, dass die Artbildung im grossen und ganzen auf anderen Wegen erfolgt als durch Bastardierung. Solche Fälle sind wohl ohne Zweifel nichts anderes als seltene Ausnahmen.» In some of his earlier works, however, WEISMANN had attempted to make amphimixis (or »Vermischung») responsible for all »the material of individual differences through which selection produces new species» (WEISMANN 1886 p. 29, comp. also 1891 p. 135), a position also accepted by WALLACE (1889 p. 439). But in this connection hybridization between different species was never mentioned, only »Vermischung» between slightly differing individuals of the same species. And with his logical mind WEISMANN realized later on, that by such »Vermischung» alone it would hardly be possible to explain the evolution in which he — contrary to KERNER — believed so strongly. On p. 175 in his last work (1913, part II) he clearly declared, that he did n o t regard amphimixis as »die eigentliche Wurzel der Variationen selbst», but considered evolution possible only by »Umbildung, Verkümmerung und Neubildung von Determinanten», *i. e.* by m u t a t i o n. — During the last two decades the hybridization-theory has got a very able and energetic advocate in LOTSY (1912—1929), who has gone further than any of his predecessors, attempting to explain e v o l u t i o n exclusively by means of

lized in the original commiscuum before the differentiation of the species concerned (comp. HERIBERT-NILSSON 1918 p. 141). — It is also known that new commiscua may be accidentally formed by the crossing of biotypes belonging to separate commiscua within the same comparium (KARPETSCHENKO 1928, DANSER 1929 *b* pp. 424—425). In the light of recent geneticists' successful production of polyploid biotypes by crossing (comp. for instance WINGE 1917, 1926 *b*, 1928, ROSENBERG 1928, RENNER 1929) it appears rather probable that the polyploid species found in many genera may have been produced by crossing of different commiscua d u r i n g the process of differentiation of the syngameon originally formed by the genus concerned (though it also looks quite possible that they have been present in the syngameon from the beginning of its existence). In this way the potential polymorphy of certain commiscua may be accidentally heightened during the differentiation-process. But as crossing between different c o m p a r i a is absolutely excluded, the potential polymorphy of a c o m p a r i u m can never be heightened, only reduced (DANSER 1929 *b* pp. 427— 428). As a comparium only rarely includes more than one g o o d genus, this implies that most genera (or at least genera not connected by hybrids with any other genus) can never heighten their potential variability, but only reduce it.

This view appears to be supported by the fossil evidence available in several plant-genera, *e. g.* in *Fagus* and *Quercus*. Only the example offered by *Fagus* will be discussed here. The *Fagus*-population of the Tertiary period apparently formed one widely distributed and very polymorphic syngameon (*Fagus Feroniae* Ung., comp. ETTINGSHAUSEN 1894, STOJANOFF and STEFANOFF 1929, etc.), containing all the forms of the present *Fagus*-species but dominated by other forms only appearing accidentally in the present *Fagus*-populations (»atavistic forms» in the sense of ETTINGSHAUSEN and KRAŠAN 1888—1889, comp. also KRAŠAN 1888). By isolation and reduction of polymorphy this highly polymorphic syngameon has become differentiated into the less polymorphic present species

hybridization. This was never attempted by KERNER, who did not believe in evolution, but only in »einer Umgestaltung, einer Umprägung des Vorhandenen» (1898 p. 5з6, comp. below p. 407). To this view also HERIBERT-NILSSON (1918 p. 143) returns, accepting the rest of LOTSY's theory, but declining the theory of evolution as impossible to reconcile with the results of modern genetics. Comp. also the theory of HAYATA reviewed below (pp. 405—410).

of Europe, Western and Eastern Asia, and North America, but still the characters of the dominating Tertiary forms as well as those of the other present species may crop up accidentally in some of those species. Nothing appears to be talking in favour of the assumption of a Post-Tertiary »evolution» in this genus, neither by crossing nor by mutation. If all the *Fagus*-populations now isolated in Europa, Asia, and America were brought together again into one large syngameon, it appears rather probable that we would get back much of the a c t u a l polymorphy of the Tertiary *Fagus*-population — but the p o t e n t i a l polymorphy of the genus would remain just the same, and would probably prove much lower than that of the Tertiary population.

The difficulties in reconstructing the old syngameons, from which the present species may have been differentiated and into which they may be naturally grouped, are rapidly increasing as we get along to genera or units of still higher rank. According to the very suggestive theory of LOTSY (1916, comp. also DU RIETZ 1921 p. 90), each main class of animals and plants originally formed one vast syngameon (originating from an accidental cross of widely differing biotypes of an older syngameon), but even if this be true, the reconstruction of the whole process of differentiation of those immense syngameons of decreasing size appears anyhow to be a rather hopeless task. Our division of the main classes of animals and plants into orders, families, genera etc. must therefore to a large extent be carried out in the rather artificial way of grouping the species, genera etc. simply after their morphological resemblance. The same method must often be used even for the grouping of the species within a genus, at least until the commiscua and comparia within that genus have become sufficiently known. The more this purely morphological method can be combined with geographical, paleontological, genetical and cytological methods, the greater is the chance that it will ultimately be possible to reconstruct the old syngameons within the group concerned.

According to current opinion among taxonomists and morphologists of the present day, this morphological method of delimiting taxonomical units of higher rank should be founded upon the theory of d i v e r g e n t e v o l u t i o n, *i. e.* the taxonomical units should be delimited and arranged according to their supposed p h y l o g e n y. In this p h y l o g e n e t i c m e t h o d o f t a x o-n o m y a central rôle is played by the distinction between »Organisationsmerkmale» and »Anpassungsmerkmale» (NÄGELI 1884). To

the first group (also called »indifferent» or »constitutional» cha-
racters) are referred characters supposed to have arisen indepen-
dently of the environment [by some sort of »Vervollkomnungs-
prinzip» (Nägeli 1884) or »Orthogenesis» (Haacke 1893, Eimer 1897)],
to the latter group (= the »epharmonic» or »adaptive» characters of
many authors[1]) characters supposed to have arisen as »adaptations»
to a certain environment. Taxonomical units of higher rank are
allowed to be founded only upon the former group of characters.
If two species are found to have a character of this type in common
(e. g. a floral or especially an embryological character) this is
taken as a proof of their phylogenetical relationship, and they are
placed in the same genus, family etc. But if two species are found
to have a character of the second type in common (e. g. life-form,
bud-type, or leaf-type), this is said to be a case of »epharmonic
convergence» and is considered to be of no taxonomical importance
whatever.

This distinction — and with it the whole »natural» plant-system
of the present day — of course stands or falls with the theory
of an evolution by means of mutations partly induced, and partly
not induced, by the environment. To this main theory belong
all the various evolution-theories of Darwin, Nägeli, and modern
neolamarckists of selectionistic or anti-selectionistic type. Even
in the theory of evolution only by means of selected non-induced
mutations (i. e. the pure selection-theory of Weismann, comp. above
p. 401), it is hard to conceive how that distinction could be upheld
strictly. And in the theory of »evolution by means of hybridi-
zation» there is certainly no room for it at all; according to Lotsy
(comp. also Heribert-Nilsson 1918 p. 135, Du Rietz 1921 p. 90)
phylogeny is a mere illusion, »no science but a product of phantastic
speculation» (Lotsy 1916 p. 140) — and certainly nobody could be
more competent a judge in this question than Lotsy, who has devoted
a considerable part of his life to the reconstruction of phylogeny
after orthodox lines. It is just the same in the anti-evolutionistic
succession-theory of Hayata and his predecessors (Kerner etc.,
comp. below p. 407). But as practically all the leading botanical
taxonomists of the last half century have strongly believed in the
theory first mentioned, all that has been of no moment whatever.

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[1] Both those terms are sometimes used also for p h e n o t y p i c a l characters
(comp. Diels 1921 p. 137, Cockayne and Allan 1927 pp. 263—267). These, of
course, do not concern us here.

Considering the attitude of intense distrust taken by most geneticists of the present day towards the theory of mutations induced by the environment, the method of making this theory a fundament of higher botanical taxonomy may be called at least a rather dangerous one. And this will still more be the case, considering that the doubts of the geneticists are supported by the results of ecological field-studies. As was mentioned above (p. 400), my own comparative field-studies of life-forms, bud-types, leaf-types etc. in widely differing parts of the world have brought me to the conviction that such characters — belonging to the typical »epharmonic characters» (or »Anpassungsmerkmale») of orthodox taxonomy — are mostly far less correlated with the environment than generally believed. Certainly this does not speak in favour of their formation by means of mutations induced by the environment. The material upon which those statements are based cannot be presented here, but I hope soon to have it ready for publication.

A most remarkable revolt against the traditional phylogenetic method of taxonomy was started about a decade ago by B. HAYATA (Professor at Tokyo Imperial University and Director of the University Botanic Gardens), whose imposing taxonomical knowledge and wide field-experience of tropical, subtropical, and temperate vegetation certainly ought to make European botanists read his contributions (HAYATA 1921 *a*, *c*, 1928 *a*, *b*, *c*) with greater attention than appears to have been the case until now. But certainly they are revolutionary enough to make an orthodox phylogenetical taxonomist shudder. Some extracts of HAYATA's works will probably be the best way to demonstrate the main views of this remarkable reformator.

»As I stated in the preceding paper, I have been reflecting on a system of natural classification to which my attention was drawn during the score of years that I devoted to the study of the flora of Formosa. Current opinion demands that such a natural system be a static one like BENTHAM-HOOKER's or ENGLER's and that there is possible only one true ideal system, to which, however, we are as yet far from attaining, as but one phylogenetic tree is possible. Much against my will, I have come to entertain strong doubts as to the effectiveness of the modern systematizers' effort to attain the ideal system; and my twenty year's experience in systematic botany has steadily led me into quite a different

channel of thought. This I now venture to make public, though I am aware that it will meet with a great deal of opposition.

All systematizers regard the natural system as a static one with a definite form and believe that all species, genera or families have their fixed natural positions, so as to be arranged between this and that, according to their natural relations. My idea is quite different from this current opinion. I regard the natural system as a dynamic one, changing with the view of the systematizer and subject to alteration, according to the way in which it is considered, and I believe that none of the species, genera or families has a fixed natural position, but has changeable positions, subject to alteration according to the criterion for comparison. It is neither natural nor necessary that a species should in all cases be arranged between this limit and that; but should be placed between this and that according to one view, or between another this and another that according to another view. In the present paper, it is my desire to explain what I propose to call the dynamic system showing the natural relations of plants.» (HAYATA 1921 *b* pp. 97—99.)

HAYATA strongly objects against the orthodox view that only two main theories about the origin of species are possible, namely the theory »that all the species are created by God separately and independently» and the theory »that all the species are formed by evolution from a single origin», *i. e.* the evolution theory. He points out that there is »one more way possible for the formation of species», namely that »an innumerable number of species of organic beings have existed from the eternal past and will exist to the eternal future; they unite with or separate from one another, and produce many different organisms by different combinations of the genes; or they change by themselves, as the genes change» (HAYATA 1921 *a* p. 94). To this theory HAYATA gives the name of the p a r t i c i p a t i o n t h e o r y[1], and explains the theory more fully in the following way:

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[1] To the first part of this theory HAYATA later on (1928 *a*) gave a separate name, namely »the succession theory». While the participation-theory *sensu stricto* appears to be possible to reconcile with the evolution-theory in the form given to it by LOTSY, t h e s u c c e s s i o n - t h e o r y s t a n d s i n c l e a r o p p o s i t i o n t o a n y f o r m o f t h e e v o l u t i o n - t h e o r y. According to the evolution-theory, the organic population of the present day has been produced by d i v e r g e n t e v o l u t i o n, starting with very primitive organisms and successively proceeding to higher ones. According to the s u c c e s s i o n -

»The theory is in fact but one theory, yet for convenience' sake I shall treat it as two, namely: — The theory of the mutual participation of the gene, and the theory of the mutual sharing of the gene. Literally speaking, the word 'participation' seems to express a united action of genes to produce a certain result. Different

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t h e o r y, on the other hand, a divergent evolution from lower to higher organisms has not been proved, but only a succession without progression, and there is no reason to believe that the original organic population of the earth was less manifolded and of a »lower» type than the present one. — Like the hybridization-theory (comp. above p. 400), this theory can be traced back as far as to LINNÆUS, who believed in the transformation of species, and to some extent even of genera, by means of hybridization (comp. above p. 400), but certainly not in any evolution. Similar views were widely spread among the botanists of the first half of the last century — in spite of the traditional tale of evolutionistic literature, that botanists before DARWIN believed that all the present species were unchangeable, simultaneously created by God independently and separately. In 1820, W. HERBERT (comp. above p. 400) formulated the theory »that in the early periods of the world, there existed only the distinct genera of plants, or heads of families, not, however, exactly according to the present divisions of Botanists; who indeed, are perpetually at variance with each other, as to the features which are sufficient to constitute a variety, a species, or a distinct genus. The lapse of centuries and diversity of soil and climate have probably wrought the most wide and permanent distinction between vegetables, that have originated from a common stock, possibly even between the arborescent Ferns of the Andes, and the herbaceous inhabitants of our forests.» (HERBERT 1820 p. 16; this theory is mentioned by DARWIN in the historical introduction to the later editions of his »Origin of species».) In 1852 ELIAS FRIES — one of the leading botanical taxonomists of his time — wrote that »we now know with full certainty, that many quite different vegetation-periods have succeeded each other on earth, not a single one of our present species thus being original, but all of them being, as was observed already by the prophetic eye of LINNÆUS, *the daughters of the time* ('filia temporis')» (E. FRIES 1852 pp. 189—190. But like LINNÆUS, FRIES was inclined to accept the g e n e r a as original (pp. 191—193), and certainly never believed in any progressive evolution. Of Post-Darwinian authors clearly opposing the evolution-theory, A. KERNER takes the foremost place. His »Vermischungstheorie» (comp. above p. 401), first published in 1891, certainly comes nearer the views of HAYATA than any other previous theory: »Sie setzt voraus, dass von jeher zahlreiche verschiedene Pflanzenformen nebeneinander bestanden haben, was durch die fossilen Reste auch tatsächlich bestätigt wird. Was sich von Pflanzen aus früheren Perioden erhalten hat, weist durchgehends darauf hin, dass zu allen Zeiten eine grosse Mannigfaltigkeit von Pflanzenformen die Erde bevölkerte. Es bedurfte daher keiner Entwickelung, sondern nur einer Umgestaltung, einer Umprägung des Vorhandenen.» (KERNER 1898 p. 536.) However, KERNER never drew the taxonomical consequences of those views drawn by HAYATA, nor did he oppose the theory of natural selection,

genes participate in the effort to produce the resulting plant or plant organ. Different plants or plant organs on the other hand are found to share in the work of certain genes, or combinations of genes; or perhaps we may say that the word 'participation' points to the future, while the word 'sharing' points to the work accomplished in the past. Thus, different genes participate in the work of producing a certain result, while different plants share with one another the work of certain genes. It must be admitted, however, that my theory does not necessarily agree with that used in genetics, but is rather to be regarded as the latter theory expanded to the utmost limit.» (HAYATA 1921 *b* pp. 101—102.)

»All individuals alike possess innumerable genes or factors. The former present various phenomena according as, on the one hand, the latter are potent or latent; and on the other, according to the different combinations or segregations of potent genes. Consequently, the relation of one individual to the others in phenomenal appearance is the relation of mutual participation or sharing of potent and latent genes in individuals.

Then, too, all genes in individuals may be apparent at one time and latent at another, and may change their characters, according to conditions. As genes change, so change individuals. Yet, no new gene is ever created or produced; no existent gene ever vanishes. The genes now present are those that have existed from the eternal past and will continue to exist throughout the infinite future.» (HAYATA 1921 *b* pp. 102—103.)

»As for mankind, and especially for any one human family, a genealogy is the history of descent from an ancestor. The customary manner of making up a genealogy for a family is to trace its history through descent on the father's side, only one side being taken into consideration, if not the father's, then the mother's. Thus, a genealogy is usually considered to be something like a tree with spreading branches, the ancestor being here compared to the trunk, and the descendants, to the branches. It is clear that this graphical method is altogether useless when descent through both parents is taken into consideration.» (HAYATA 1928 *b* p. 1869.)

»From the Participation Theory, it follows now that it becomes, in any case, impossible to admit the existence of a single or a few forms of a particular nature ancestral to the innumerable

species which at present we have. Ancestors should (in their phenomenal appearances) be as different from one another as are their descendants. These forefathers, varying in different ways, presumably by crossing, one being succeeded by another, must have given way to the species of the present day. Even supposing ancestors to have been much simpler than their descendants and more resembling one another, they must have potentially been sufficiently different to succeed to one generation after another.» (HAYATA 1928 *c* p. 1883).

The practical application of »the dynamic system» is demonstrated by HAYATA by the following general introduction:

»Now, turning back our attention to what we have said before of the natural classification, we now see that our first attempt in the course of the latter is to find how species share their genes with others. Then, the second attempt is to group species into small or large groups according to the extent with which they have shared their genes with others [LOTSY, P. J. — Evolution by Means of Hybridization (1916) pp. 137—138], — into groups which should be subject to alteration, as to their limits as well as their members, according to whether we select this or that gene as a criterion for classification, — simply speaking, into dynamic groups. Finally, our third attempt is to arrange the dynamic groups thus obtained, such as species, genera or families, according to the relations of the mutual sharing of genes, — to arrange them, not in a fixed order, but in orders varying with views, or simply speaking to arrange them in a dynamic manner. The arrangement in dynamic forms is what I have spoken as a dynamic system. I shall explain it with examples further on.

Now, let us take four individuals representing four different species. These four are composed of numerous different genes; but amongst the latter genes only four, represented symbolically by **a, b, c** and **d,** are so far known to us. We shall try to systematize these species. Let a gene in parentheses denote a latent gene. Then, the four species may be symbolized as follows: — (a)bcd, a(b)cd, ab(c)d and abc(d). One way of classifying these four is to group them into two groups, one containing the latent (a) gene and the other, the potent **a** gene. There are more three different ways of making up such groups of the same category by substituting (b) (c) or (d), in the place of (a). Also, there are certainly many other ways of grouping the four species so as

to classify the species by taking a combination of genes as a criterion instead of a single gene, such as **ab, cb, ac, bc, cd,** or **bcd, acd, abd, abc,** and so forth, — each way being in agreement with a natural relation according to each respective view. So the groups themselves are changeable or dynamic, according to whether we take this gene or that, or this combination or that, as a criterion for classification. One way of grouping can not be said to be more natural than others. Any one is natural so far as it is understood as dynamic and changeable according to views. But as soon as it is understood to be the only fixed, unchangeable one, admitting no other way, it becomes unnatural.» (HAYATA 1921 *b* pp. 105—106).

After this introduction HAYATA demonstrates his principles more in detail by presenting a »dynamic system of natural classification applied to the Angiosperms, with ENGLER's system as a framework.» (HAYATA 1921 *b* pp. 159—216). Everyone of ENGLER's orders and families is put in the centre of those families to which, according to HAYATA, it shows a distinct relationship. As to this practical application of the system, however, I must refer the reader to the original treatise.

I have quoted HAYATA's work to such a length because his views appear to have been unduly overlooked by most present-day taxonomists [the only reference to them that I have seen is the reviews of KRAUSE (1922 *a, b*) and a few words by CROW (1926)], and also because those views are very similar to those in which my own field-experience has resulted. When I learnt to know HAYATA's works in 1929, I was really surprised to find how my own field-experience, culminating in my voyage around the world in 1926—1927, had brought me to views in many respects identical with those expressed by HAYATA several years earlier (DU RIETZ 1929 pp. 421—422). I am mentioning this because I fully realize what opposition those views will meet, and because I must take it as a good sign that they have crystallized independently in the minds of two botanists with wide field-experience in widely differing parts of the world's vegetation.

When my own field-studies had brought me to the conviction that the »epharmonic characters» (»Anpassungsmerkmale») did not show the high degree of correlation with the environment postulated in orthodox taxonomy and ecology, I could not help drawing the conclusion that the method of founding the higher taxo-

nomical units only upon the traditional »Organisationsmerkmale» could not be maintained. The conflict with the traditional system arising from this consideration brought me to try various alternatives for the grouping of the species in certain genera. During those attempts I discovered some remarkable regularities in the geographical distribution of various characters. Studying the New Zealand flora, for instance, I found that in the genus *Celmisia* brown and yellow hairs showed a remarkable frequency in the northern part of South Island, being found there in species widely differing in other respects (*C. Traversii, C. cordatifolia, C. Macmahoni, C. Dallii,* and *C. hieracifolia*), but of much rarer occurrence in other parts of New Zealand. In the genus *Dracophyllum* similar regularities were found (comp. above p. 398): terminal panicles or racemes are found in many species of the northern and central part of North Island (from the small dwarf-shrub species *D. recurvum* to the big tuft-tree species *D. latifolium, D. recurvatum* etc.) but only in one species of South Island (*D. Traversii*) and in no species at all in the southern part of South Island, where lateral panicles or racemes are characteristic even in the large-leaved tuft-tree species *D. fiordense* (comp. OLIVER 1928). In the genus *Euphrasia* I found that digitate leaves (a character found in all the South American species of that genus but very rare elsewhere) were characteristic for several species (rather different in other respects) of the southern part of South Island, but in the rest of the Australian-New Zealand region only occured in one Tasmanian species (comp. WETTSTEIN 1896 *b*), *i. e.* that this South American character was found in widely differing species only in the parts of Australasia geographically most related to South America. In the same genus I found certain life-forms concentrated to certain parts of New Zealand, where they could impossibly be correlated with a certain climate, but in those parts appearing in the most different groups of the genus (just the same if those groups were founded upon the flowers or upon the leaves). — To all those regularities (and many others that cannot be mentioned here) I could not find any other possible explanation than that in the syngameon originally formed by each of those genera, certain genes had been generally distributed only in certain districts, but in those districts had »infected» the whole population. In this respect there was no difference whatever in the behaviour of »Organisationsmerkmale» and »An-

passungsmerkmale» in the traditional sense. But if »epharmonic characters» could behave in this way within a certain genus, it did not then look impossible that they could do the same also in larger populations, *i. e.* that many cases of »epharmonical convergence» could be explained simply by the accidental distribution of a certain gene in the whole population formed by a certain family, order or even class in a certain region already at the time when this population formed o n e vast syngameon.

Just the same point of view may be applied to the many examples known of »Vavilov's law of homologous variation» (comp. above p. 346). If homologous forms appear in species belonging to quite different genera or families, why may not this simply be the result of the presence of the same gene in all those forms? For nearly related species this explanation already appears to be generally accepted among geneticists (comp. Philiptschenko 1927). But as soon as we come to species belonging to different higher units of the traditional system, Philiptschenko finds its impossible to apply this theory of »genotypical parallelism», postulating a principially different »morphological parallelism», »auf deren Eigentümlichkeiten der Begriff der Gene und der genotypischen Struktur überhaupt nicht anwendbar ist» (Philiptschenko 1927 pp. 74—75.) As an intermediate type of parallelism Philiptschenko accepts the »oecotypical parallelism», which »bald von gleichen, bald auch von völlig verschiedenen genotypischen Strukturen abhängen kann» (l. c.). As a result of this negative attitude towards the explanation of the »morphological parallelism» Philiptschenko finds it possible to explain only »the evolution of biotypes, jordanons and linneons», or the »micro-evolution» in the light of modern genetics, while he considers »the evolution of higher taxonomical groups» or »macro-evolution» to lie completely »ausserhalb ihres Gesichtsfeldes» (pp. 93—94). May be he is right, but certainly my own experience makes me more inclined to follow Hayata in looking for the explanation also of »morphological parallelism» in genotypical resemblance.

Of course we must not forget that it is not allowed to translate »character» into »gene». We can only see the characters but not the genes, and a certain character is supposed to be the result of the coaction of an immense number of genes, a l l of which are necessary for the formation of the character. The disappearing of a certain character may thus be the result of the lack of quite

different genes in different cases, and vice versa (comp. for instance JOHANNSEN 1913 pp. 666—667, and especially the very clear discussion by HAGEDOORN 1921). The matter looks still more complicated in the light of GOLDSCHMIDT's (1920, 1928) theory of q u a n t i t a t i v e gene-differences. Future research must show to what extent those difficulties may be overcome in practical taxonomy. Theoretically we may attempt to follow the suggestion of HAYATA to found the higher units of taxonomy upon the distribution of genes, but practically it looks quite possible that we will still have to be content with founding them upon the distribution of c h a r a c t e r s. Anyhow, the main reform that is needed in higher taxonomy certainly is that we will have to take genotypical characters as they are without any subjective valuation, neither in »Organisationsmerkmale» and »Anpassungsmerkmale» nor in »progressive» and »regressive» characters. And here HAYATA certainly is right both in pointing out that every natural system must form a n e t w o r k and not a phylogenetical tree,[1] and in rejecting the idea of o n e single static system.

My main objection against the principles of HAYATA is that I think he is underrating the taxonomical importance of the lines or zones of discontinuity formed in the series of biotypes by geographical, ecological or physiological isolation. As has been the main purpose of this paper to show, I think that t h e f u n d a m e n t a l u n i t s of taxonomy should be founded just upon those lines or zones of discontinuity, and the purely morphological grouping taken as a refuge first when we proceed to populations of higher rank in which that method is failing. I am also more inclined than HAYATA to leave the question open whether »no new gene is ever created or produced» and whether »no existent gene ever vanishes». How life originated on earth »in the eternal past» we shall probably never know, nor how it will develop or if it will even exist »in the eternal future».

But with those restrictions (and perhaps some others of minor importance), I feel convinced that the participation theory and the dynamic system of HAYATA will prove a most excellent working-base for the great reform of higher botanical taxonomy that is so greatly needed. I cannot refrain from citing in this connection the following critical remarks made by KRAUSE in his review of

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[1] DIELS (1921 pp. 187—189) has also pointed out, that the relationship of plants is far better illustrated by a network than by the traditional phylogenetical tree.

HAYATA's first work on those subjects, because they give the best characteristic possible of the prejudices dominating present taxonomical botany:

»Die angeführten Proben zeigen, dass Verf. einmal Analogien, wie z. B. Anordnung der Blüten in Kolben, erikoide Blattgestalt, ähnliche Fruchtentwicklung, Kleinheit der Samen usw. als Grundlagen für die Annahme einer natürlichen Verwandtschaft ansieht. ... Denn nicht selten hat man den Eindruck, als ob Verf. rein äusserliche, vielleicht nur durch gleiche Lebensverhältnisse bedingte Ähnlichkeiten, wie Blattform, Sukkulenz oder dergleichen, auf eine Stufe stellt mit anderen wesentlichen Merkmalen im Blütenbau, wie Beschaffenheit und Stellung der Samenanlagen usw.» (KRAUSE 1922 *a* p. 51).

I do not think that the fundamental difference between the view of HAYATA and myself and that of traditional taxonomy could have been expressed better. For my own part, it is just in the raising of those neglected »epharmonic characters» (or »Anpassungsmerkmale») to the same taxonomical rank as that so long monopolized by the floral characters only, that I see the only way to an unprejudiced study of the higher taxonomical units. But HAYATA's excellent idea of the dynamic system certainly ought to make it possible for old and new systems to exist in friendship side by side in future taxonomy.

Plantbiological Institution of Upsala University, June 25th, 1930.

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CONTENTS.

Postscript.

During the printing of this paper there has appeared a new paper of N. HERIBERT NILSSON (Sind die mutierenden reinen Linien auch rein?, Hereditas, Bd. XIV, H. 1, Lund 1930), containing such importants results and views that I cannot refrain from adding a few words about them. By extensive cultures HERIBERT NILSSON has found that different individuals of a certain so-called »pure line» of oats produce pure lines differing considerably in their production of »mutations», some of them giving a much higher percentage of mutations than others. From this result HERIBERT NILSSON draws the conclusion that the original »pure line» did not contain only homozygous individuals, thus being no real pure line at all, and that the »mutations» appearing in it

(and in analogous false pure lines) are no real mutations but simply some sort of »segregants» caused by the heterozygosity. This certainly does not speak in favour of the current theory of the rapid production of pure (*i. e.* homozygotic) lines by autogamous reproduction (comp. above p. 339). On the contrary, it gives a strong support to Lotsy's recent doubting of the existence of any absolutely homozygotic biotype in nature even in »pure lines» (comp. above p. 341). This implies that the existence of real pure lines in nature may be a mere illusion, and that the taxonomical importance of the pure line-concept thus would be still smaller than postulated above (p. 339).